

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 dDifferent 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 diff A simulated area closure showed that aAggregation across time periods has less of a negative impact on the closure success than aggregation over space. -and wWhile 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.

MixFishSimOur 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 wWhile 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 wWe 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 characteristics of the different processes (Figure 1).
88 The following sub-modules were included to capture the full system comprised:
89 1) pPopulation dynamics, 2) rRecruitment dynamics, 3) pPopulation movement,

90 4) fishery 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 ~~that~~which models the fish popula-
 101 tions in terms of aggregate biomass of recruits and mature components rather
 102 than keeping track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al.,
 103 2003). A daily time-step was chosen to discretise continuous population pro-
 104 cesses on a biologically relevant and computationally tractable timescale. Popu-
 105 lation biomass growth was modelled as a function of previous recruited biomass,
 106 intrinsic population growth and recruitment functionally linked to the adult
 107 population size. Biomass for each cell c was incremented each day d as follows
 108 (~~see the full parameter list is detailed in~~ Table 1 for all parameter details):

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

109 where ρ is Brody's coefficient, shown to be equal to e^{-K} when K is the growth
 110 rate at which the asymptote is approached from a von Bertalanffy logistic growth
 111 model (Schnute, 1985). Wt_{R-1} is the average weight of fish prior to recruit-
 112 ment, while Wt_R is the average recruited weight [CM: do we need Wt or can
 113 we just use W ? Use mass instead of weight?]. α_d represents the proportion of
 114 fish recruited during that day for the year, while $R_{c,\tilde{y}(c)}$ is the annual recruits

115 in year y for cell c .

116

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

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

121 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and
 122 vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass
 123 for the population in the cell. Here, catch is the sum of those across all fleets
 124 and 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
 125 total number of fleets, v and V the vessel and total number of vessels respec-
 126 tively [CM: do we want to allow for different numbers of vessels per fleet? If
 127 so, use V_{fl} for the upper limit] and $E_{fl,v,c,d}$ and Q_{fl} fishing effort and catcha-
 128 bility of the gear, and $D_{c,d}$ is the density of the population at the location fished.

129

130 2.2. Recruitment dynamics

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

$$\bar{R}_{c,d} = \frac{(\alpha \cdot S_{c,d})}{(\beta + S_{c,d})} \quad (3)$$

$$\ln(R_{c,d}) \sim \text{logN}[(\ln \bar{R}_{c,d}), \sigma^2]$$

135 [CM: Do we include a bias correction? If not the first term is the median,
 136 which is fine, just not the mean] where α is the maximum recruitment rate,
 137 β the spawning stock biomass (SSB) required to produce half the maximum
 138 stock size, S current stock size and σ^2 the variability in the recruitment due to

139 stochastic processes. The stochastic Ricker form (Ricker, 1954) is [CM: edit as
140 above]:

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

141 where α is the maximum productivity per spawner and β the density depen-
142 dent [CM: hyphenate?] reduction in productivity as the SSB increases.

143 2.3. Population movement dynamics

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

151

152 The combined process results in a population structure and movement pat-
153 tern unique to each population, with population movement occurring on a
154 weekly basis. MThe decision to modeling population movement on a weekly
155 timescale was to reflect that fish tend to aggregate in species-specific locations
156 that have been observed to last between around one and two weeks (Poos and
157 Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts
158 in fish populations throughout a year with seasonal spawning patterns (Figure
159 S7)[CM: shouldn't it be S1 so that the they follow the main ms? Maybe not
160 ...].

161 To simulate fish population distribution in space and time a Gaussian spa-
162 tial process was employed to model habitat suitability for each of the popula-
163 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
164 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
165 $\{S(c_1), \dots S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,

166 where the correlation strength weakens with distance controlled by two param-
 167 eters, with ν a scale parameter in the units of distance and κ a shape parameter
 168 which determines the smoothness of the process. We use the most commonly
 169 used Matérn covariance structure as it is a flexible form that contains the under
 170 ~~certain conditions is of the same form as an~~ exponential and double exponen-
 171 ~~tial as special cases function and it~~ This enables us to model the spatial au-
 172 tocorrelation observed in animal populations where density is more similar in
 173 nearby locations, ~~but that correlation decreases non-linearly~~ (Tobler, 1970; F.
 174 Dormann et al., 2007; Poos and Rijnsdorp, 2007b). We change the parameters
 175 to implement different spatial structures for the different populations using the
 176 *RandomFields* R package (Schlather et al., 2015). We define a stationary habi-
 177 tat field with an anisotropic pattern (to simulate a depth gradient) and combine
 178 it with a temporally dynamic thermal tolerance field to imitate two key drivers
 179 of population dynamics without modelling the processes explicitly. Each pop-
 180 ulation was initialised at a single location, and subsequently moved across the
 181 entire space according to a probabilistic distribution based on habitat suitability
 182 (represented by the normalised values from the GRFs), temperature tolerance
 183 and distance from current cell:

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

184 Where $d_{I,J}$ is the euclidean distance between cell I and cell J , λ is a given rate
 185 of decay, $Hab_{c,p}$ is the index of habitat suitability for cell c and population p ,
 186 with $Tol_{c,p,wk}$ the temperature tolerance for cell c by population p in week wk
 187 (see below).

188
 189 During pre-defined weeks of the year the habitat suitability is modified with
 190 user-defined spawning habitat locations, resulting in each population having
 191 concentrated areas where spawning takes place. The populations then move to-
 192 wards these cells in the weeks prior to spawning, resulting in directional move-
 193 ment towards the spawning grounds.

194

195 A time-varying temperature covariate changes the interaction between time
 196 and suitable habitat on a weekly time-step. Each population p was assigned a
 197 thermal tolerance with mean, μ_p and standard deviation, σ_p so that each cell
 198 and population temperature tolerance is defined ~~asthat~~:

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

199 Where $Tol_{c,p,wk}$ is the tolerance of population p for cell c in week wk , $T_{c,wk}$ is
 200 the temperature in the cell given the week and μ_p and σ_p the mean and stan-
 201 dard deviation of the population temperature tolerance. The variables, their
 202 meaning and units for population movement is provided in Table 2.

203

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

211 2.4. Fleet dynamics

212 Fleet dynamics ~~werecan be~~ broadly categorised into three components. *Fleet*
 213 *targeting* ~~determineddetermines~~ the fleet catch efficiency and preference to-
 214 wards a particular population; *trip-level decisions* ~~determinedthat determines~~
 215 the initial location to be fished at the beginning of a trip; and *within-trip deci-*
 216 *sions* ~~determined fishing locations, that determines movement from one fishing~~
 217 ~~spot to another~~ within a trip. This results in an explore-exploit strategy ~~was~~
 218 ~~implemented in the model that combined these three components~~ for individual
 219 vessels to maximise their catch from an unknown resource distribution (Bailey
 220 et al., 2019). The decision to use an individual based model for fishing vessels
 221 was taken because fishers are heterogeneous in their location choice behaviour

222 due to different objectives, risk preference and targeting preference (Van Putten
223 et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics
224 are emergent from individual dynamics rather than pre-defined group dynamics.

225 *2.4.1. Fleet targeting*

226 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
227 and a population specific efficiency, $Q_{fl,p}$ which are each bound by $[0,1]$. The
228 product of these parameters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet
229 and the preferential targeting of one species over another. This, in combination
230 with the parameter choice for the step-function defined below (as well as some
231 randomness from the exploratory fishing process) determined the preference of
232 fishing locations for the fleet.

233 *2.4.2. Decision about where to fish at the start of a trip*

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

244 *2.4.3. Decision about where to fish within a trip*

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

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

258

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

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

265 where $L_{c,d,p}$ is landings of a population p , and Pr_p price of a population. All
 266 population prices were kept the same across fleets and seasons. Here, when
 267 fishing is successful vessels remain in a similar location and continue to exploit
 268 the local fishing grounds. When unsuccessful, they move some distance away
 269 from the current fishing location. The movement distance retains some degree
 270 of stochasticity, that can be controlled separately, but is determined by the
 271 relationship:

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

272 Where β_1 , β_2 and β_3 are parameters determining the shape of the step function
 273 in its relation to revenue, so that, a step from (x_t, y_t) to (x_{t+1}, y_{t+1}) is defined

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

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

275 where Le is the step length, Br_t is the bearing at time t , k the concentration
 276 parameter from the von Mises distribution that we correlate with the revenue so
 277 that $k = (Rev + 1/RefRev) \cdot max_k$, where max_k is the maximum concentration
 278 value, k , and $RefRev$ is parametrised as for β_3 in the step length function.
 279 Details of the variables, meaning and units for fleet dynamics are provided in
 280 Table 3.

281 2.4.4. Local population depletion

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

291 2.5. Fisheries independent survey

292 A fisheries-independent survey is simulated where fishing on a regular grid
 293 begins each year at the same time for a given number of stations (a fixed station
 294 survey design). Catches of the populations at each station are recorded but not
 295 removed from the population (catches are assumed to have negligible impact
 296 on population dynamics). This provides a fishery independent snapshot of the

297 populations at a regular spatial intervals each year, similar to scientific surveys
298 undertaken by fisheries research agencies.

299

300 2.6. Software: R-package development

301 The simulation framework is implemented in the statistical software package
302 R (R Core Team, 2017) and available as an R package from the author’s github
303 site (www.github.com/pdolder/MixFishSim).

304

305 3. Model calibration

306 We calibrate *MixFishSim* to investigate the influence of data aggregation on
307 spatial inference.

308 3.1. Population models

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

320 3.2. Fleet calibration

321 The fleets were calibrated to reflect five different characteristic fisheries with
322 unique exploitation dynamics (Table 5). By setting different catchability coef-
323 ficients ($Q_{fl,p}$) we create different targeting preferences between the fleets and

hence spatial dynamics. The learned random walk process implies that within a fleet different vessels have different spatial distributions based on individual experience. The step function was calibrated 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).

Fishing locations were chosen based on random search and, with increasing proportion as time progressed, 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 revenue from previous trips 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 that 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 parameter ($Q_p = 1$) for all populations p . 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 100×100 square grid (undetermined units), with

353 five fleets of 20 vessels each and four fish populations. Fishing takes place four
354 times a day per vessel and five days a week, while population movement is every
355 week.

356

357 *How does sampling-derived fisheries data reflect the underlying population*
358 *structure?*

359

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

362 a) **fisheries-independent data:** the inferred population density from a
363 fixed-site sampling survey design as commonly used for fisheries monitor-
364 ing purposes;

365 b) **fisheries-dependent data:** the inferred population density from our
366 fleet model that includes fishery-induced sampling dynamics.

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

371

372 The following steps are undertaken to determine closures:

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

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

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

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

394 4. Results

395 4.1. Emergent simulation dynamics

396 Individual habitat preferences and thermal tolerances result in different spa-
397 tial habitat use for each population (Figure S1) and consequently different sea-
398 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.

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

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

405 *4.2. How does sampling-derived fisheries data reflect the underlying population* 406 *structure?*

407 The ~~aggregated~~ catch composition ~~aggregated at different spatial resolutions~~
408 from each of the data sources (~~which shows~~ average seasonal patterns over a
409 ten-year period) highlights different patterns in perceived community structure
410 depending on the data source and aggregation level (Figure 3). The finer spatial
411 grid for the true population (top left) and commercial data (top middle) show
412 visually similar patterns, though there are large unsampled areas in the com-
413 mercial data from a lack of fishing activity (particularly in the lower left part
414 of the sampling domain). The survey data at this spatial resolution displays
415 very sparse information about the spatial distributions of the populations. The
416 slightly aggregated data on a 5 x 5 grid shows similar patterns and, while los-
417 ing some of the spatial detail, there remains good consistency between the true
418 population and the commercial data. Survey data starts to pick out some of the
419 similar patterns as the other data sources, but lacks spatiotemporal coverage.
420 The spatial catch information on a 10 x 10 and 20 x 20 grid lose a signifi-
421 cant amount of information about the spatial resolutions for all data sources,
422 and some differences between the survey, commercial and true population data
423 emerge.

424
425 Different perceptions of the proportion of each stock in an area are seen when
426 we aggregate the data at different timescales, with weekly (top), monthly (mid-
427 dle) and yearly (bottom) catch compositions from across an aggregated 20 x 20
428 area showing different patterns (Figure 4). In the true population, the monthly

aggregation captures the major patterns of composition seen in the weekly data with the percentage of different populations in the catch having similar mean and standard deviations (Table 7). In the weekly and monthly data population 2 dominates. However, some of the variation was lost when aggregated to an annual level, as indicated from the lower standard deviations (Table 7).

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

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

4.3. How does data aggregation and source impact on spatial fisheries management measures?

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

In most cases the fishery closure was successful in reducing fishing mortality on the species of interest (population 3; Figure 5). Interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries “adapted” to the closures by finding new areas of high abundance to fish. This led to fishing mortality increasing again, though not to past levels (Figure 5). The exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective (i.e. failed to reduce fishing mortality) with all data sources.

459 As expected, closures based on the “known” population distribution were most
460 effective, with differing degrees of success using the commercial data. Fishing
461 mortality rates on the other species changed in different proportions, depending
462 on whether the displaced fishing effort moved to areas where the populations
463 were found in greater or lesser density.

464
465 The factor most contributing to differences in fishing mortality before and
466 after the closure was the population (72 % showing that the closures were ef-
467 fective for population 3), followed by data resolution (21 %), data type (7 %)
468 with the least important factor the timescale (< 1 %). In general the finer the
469 spatial resolution of the data used the greater reduction in fishing mortality for
470 population 3 after the closures (Figure 6). The notable outliers are the com-
471 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
472 timescale, where closures were nearly as effective as the fine-scale resolution. In
473 this case the closures were sufficiently large to protect a core area of the habitat
474 for the population, but this was achieved in a fairly crude manner by closing a
475 large area - including area where the species was not found (Figure 7) that may
476 have consequences in terms of restricting the fishery in a much larger area than
477 necessary. We found that these trade-offs existed, with high catches maintained
478 with an effective closure when the highest resolution data was used, with the
479 effect being linear when the true population distribution was known and also
480 persisting for closures based on commercial information (Figure 8).

482 5. Discussion

483 Our study presents a new highly resolved fisheries simulation framework to
484 evaluate the importance of data scaling and considers potential bias introduced
485 through data aggregation when using fisheries data to infer spatiotemporal dy-
486 namics of fish populations. Understanding how fishers exploit multiple hetero-
487 geneously 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 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

518 to those obtained under a statistical modelling framework.

519

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

531

532 Demographic stochasticity arises due to individual-level variability in time to
533 reproduction and death. This form of stochasticity is often modelled by drawing
534 random time intervals from a given distribution (Gillespie, 1977). The impact
535 of demographic stochasticity depends on the population size, with the effects
536 expected to decrease with increasing population size (Lande et al., 2010). This
537 contrasts with environmental stochasticity, which affects all population sizes
538 and is present at the population level in our model by variability in recruitment.

539

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

549 *5.2. How does sampling-derived fisheries data reflect the underlying population*
550 *structure?*

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

558
559 Our simulation shows that, despite biases introduced through the fishing
560 process, the commercially derived data could still inform on the key spatial
561 patterns in the community structures where the fisheries occurred, which was
562 spatially limited due to the “hotspots” of commercially valuable species be-
563 ing fished. Similarly, despite the even spatial coverage the survey was able to
564 capture some of the same spatial patterns as the true population, but missed
565 others due to gaps between survey stations limiting spatial and temporal cov-
566 erage (Figure 3). This provides a challenge when modelling unsampled areas in
567 inferring species distribution maps, though these limitations may be overcome
568 by understanding the relationship between the species and habitat covariates
569 where these are known at unsampled locations (Robinson et al., 2011).

571 *5.3. How does data aggregation and source impact on spatial fisheries manage-*
572 *ment measures?*

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

577

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

592
 593 Two contrasting real world approaches in this respect were the spatial clo-
 594 sures to protect cod in the North Sea. In one example, large scale spatial closures
 595 were implemented with little success due to effort displacement to previously
 596 unfished areas (Dinmore et al., 2003), while in another small scale targeted
 597 spatiotemporal closures were considered to have some effect in reducing cod
 598 mortality without having to disrupt other fisheries substantially (Needle and
 599 Catarino, 2011). These examples emphasise the importance of considering the
 600 right scale and aggregation of data when identifying area closures and the need
 601 to consider changing dynamics in the fisheries in response to such closures.

602
 603 Our study showed that fishing rates on other populations also changed (both
 604 up and down) as a side-effect of closures to protect one species. This indicates
 605 the importance in considering fishing effort reallocation following spatial clo-
 606 sures, and our simulation allows us to consider the spatiotemporal reasons for
 607 these changes.

608 5.4. Model assumptions and caveats

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

613
614 Fish populations in our simulations move in pre-defined timescales and ac-
615 cording to fixed habitat preferences and temperature gradients (Figures S3, S5).
616 Our assumptions in calibrating the model (movement rates, temperature toler-
617 ances) will have a direct impact on our conclusions on the relative importance
618 of spatial and temporal processes. These assumptions could be explored in a
619 future study by varying the parameters and assessing the robustness of our con-
620 clusions. For our example application we have chosen movement rates to reflect
621 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

622
623 In addition, we have assumed that fishing vessels are not restricted by quota
624 and therefore discarding of species for which vessels have no quota or that are
625 unwanted is not taken into account. This is likely to be a significant source of
626 bias in any inference using commercial data and should also be explored. For
627 example, *MixFishSim* could be altered to allow for spatiotemporal appraisal of
628 the impact of discarding on fisher behaviour and underlying populations via in-
629 clusion as discarding behaviour, or through move-on rules or cessation of fishing
630 activity when quota is exhausted.

632 5.5. Future applications of *MixFishSim*

633 We consider that the increased availability of high resolution catch and lo-
634 cational information from commercial fisheries will require it to be a key source
635 of data for ensuring management is implemented at the right scale in future.
636 For example, identifying hot-spots for bycatch reduction or identifying spatial
637 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

667 and identity where data collection is needed to strengthen inference.

668

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

681

682 While any findings are likely to be case specific, our findings emphasise the
683 need to understand population demographics, habitat use and movement rates
684 in designing any closure scenario based on observational sampling. This infor-
685 mation can then be used to set the bounds on data aggregation used in modelling
686 studies aimed at informing the management measures.

687

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

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701 competing interests.

702 **Appendices**

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

Variable	Meaning	Units
Population dynamics		
<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 ⁻¹
ρ	Brody's growth coefficient	yr ⁻¹
Wt_R	Weight of a fully recruited fish	kg
Wt_{R-1}	Weight of a pre-recruit fish	kg
α_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
Recruitment dynamics		
$\tilde{R}_{c,d}$	is the recruitment in cell c for day d	d^{-1}
$B_{c,d}$	biomass in cell c for day d	d^{-1}
α	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	kg
β	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	$^{\circ}\text{C}$
μ_p	Mean of the thermal tolerance for population p	$^{\circ}\text{C}$
σ_p	Standard deviation of thermal tolerance for population p	$^{\circ}\text{C}$
<i>Population movement model</i>		
λ	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	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg^{-1}
Le	Step length for vessel	-
Br	Bearing	degrees
k	Concentration parameter for von mises distribution	-
β_1	shape parameter for step function	-
β_2	shape parameter for step function	-
β_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 ν	1/0.015	1/0.05	1/0.01	1/0.005
Matérn κ	1	2	1	1
Anisotropy	1.5,3,-3,4	1,2,-1,2	2.5,1,-1,2	0.1,2,-1,0.2
Spawning areas (bound box)	40,50,40,50; 80,90,60,70	50,60,30,40; 80,90,90,90	30,34,10,20; 60,70,20,30	50,55,80,85; 30,40,30,40
Spawning multiplier = 10				
Movement $\lambda = 0.1$				
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit α	6	27	18	0.3
Beverton-Holt Recruit β	4	4	11	0.5
Beverton-Holt Recruit σ^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				
μ_p	12	15	17	14
σ_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 β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_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)

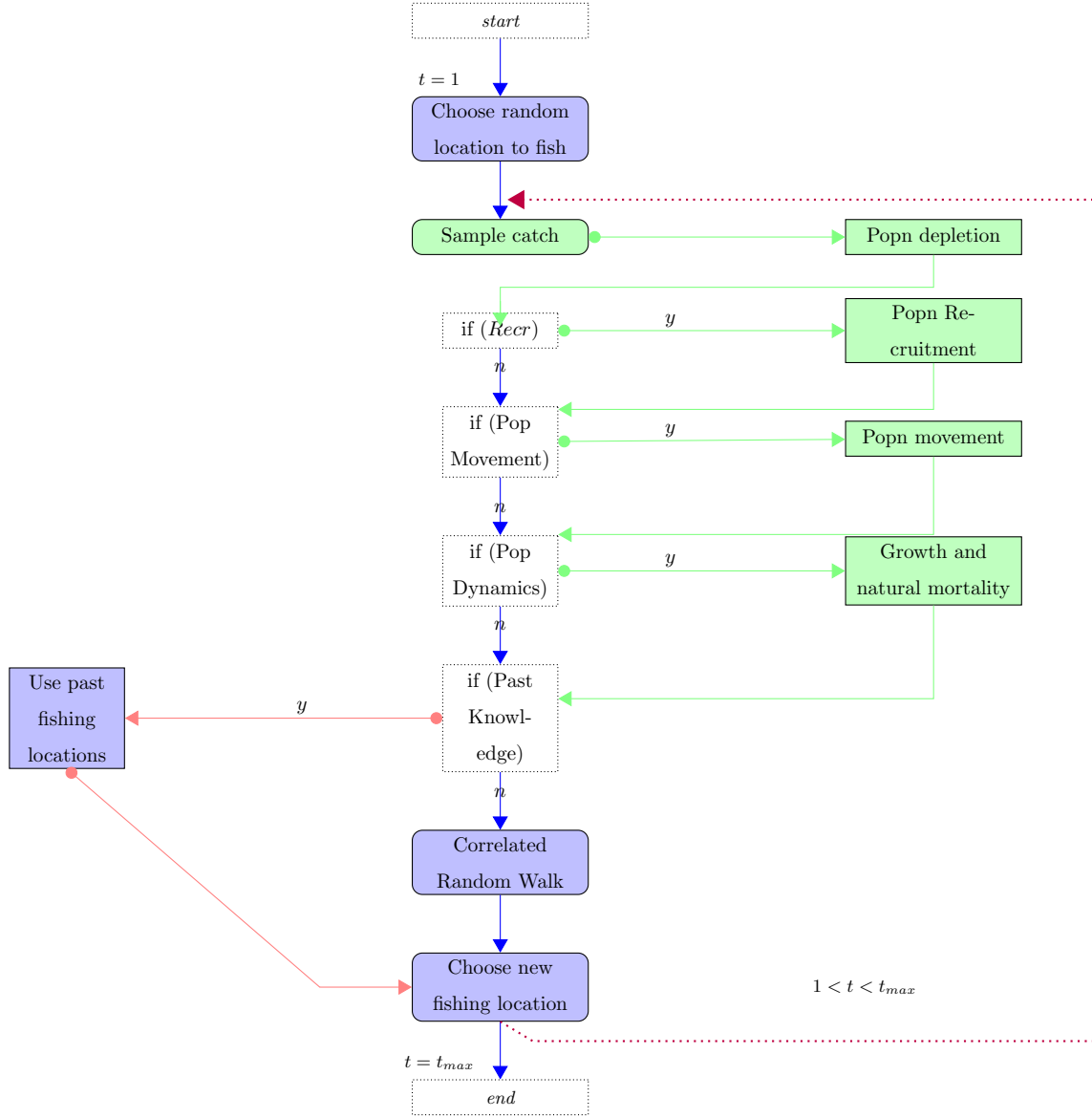


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (*Recr*), (*Pop Movement*), (*Pop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

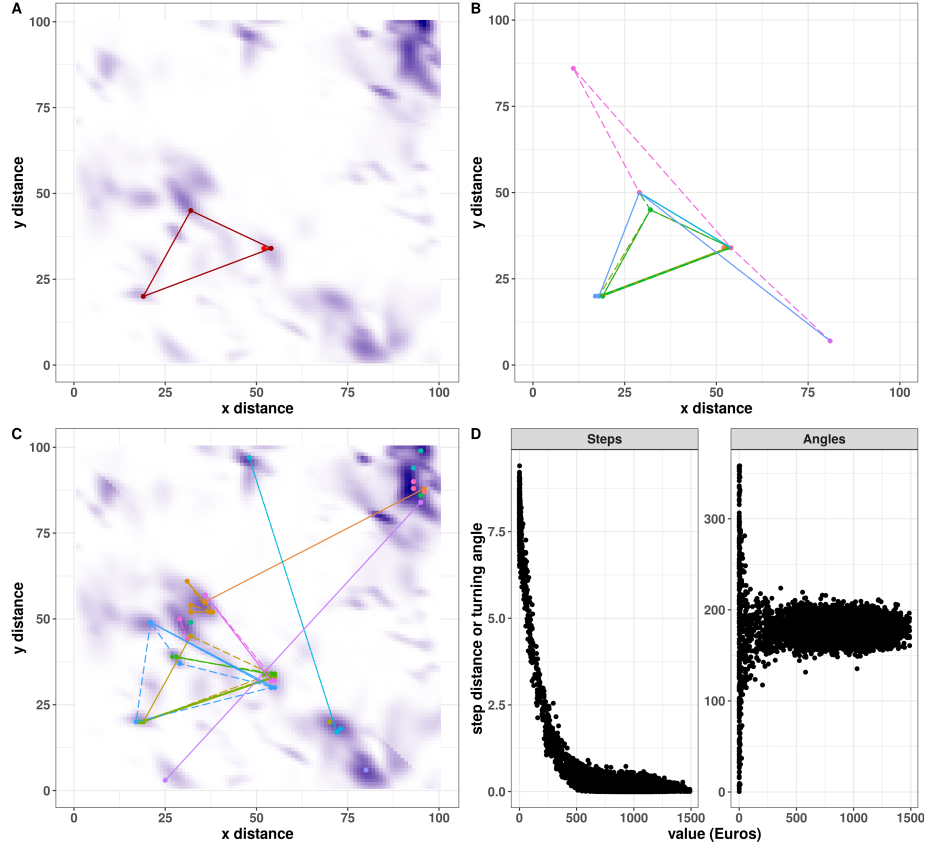


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not 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.

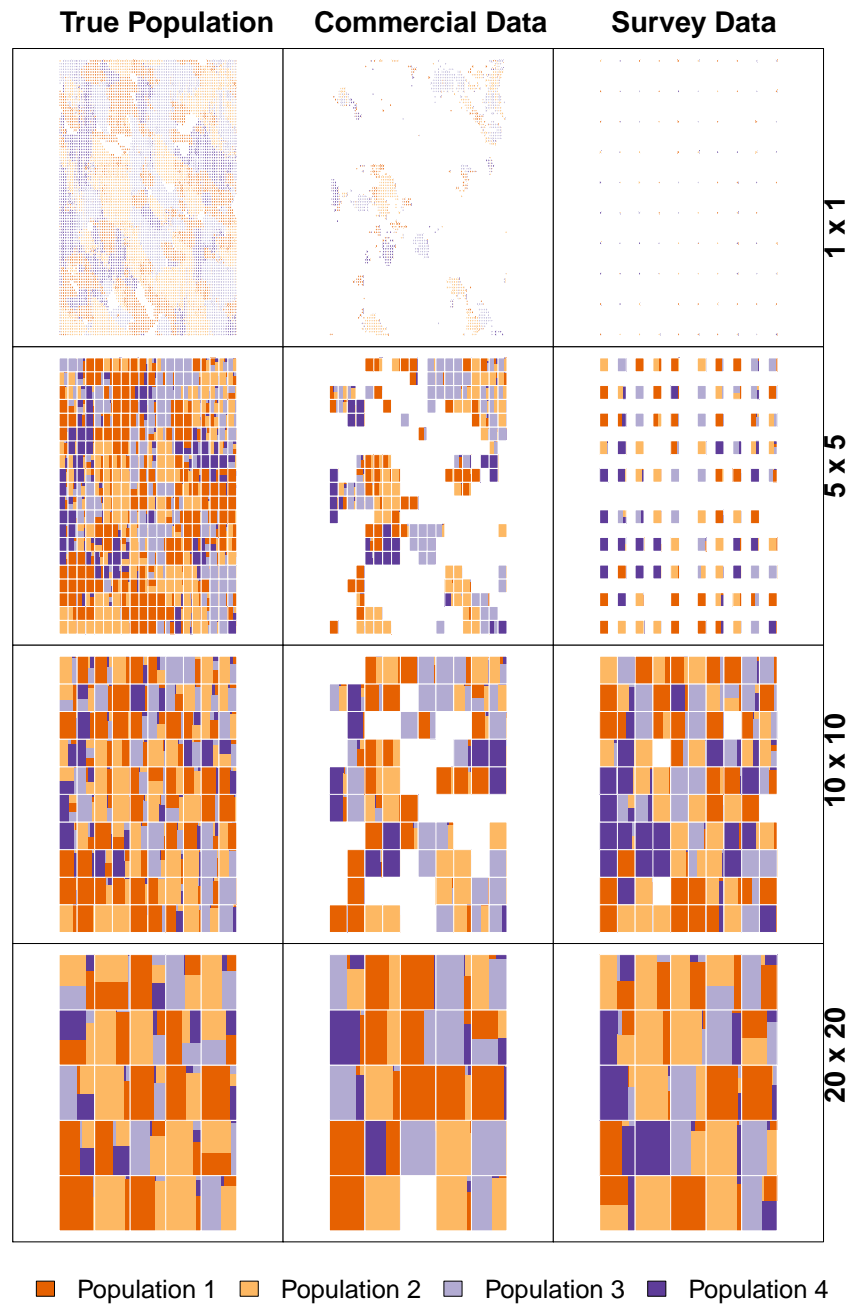


Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit.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

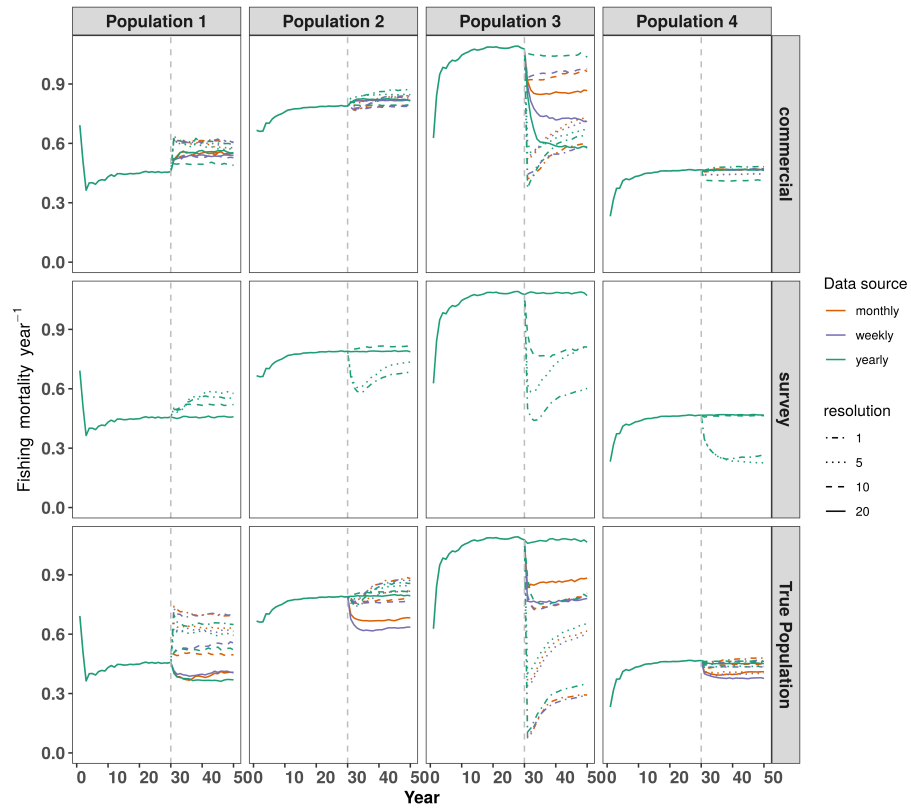


Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

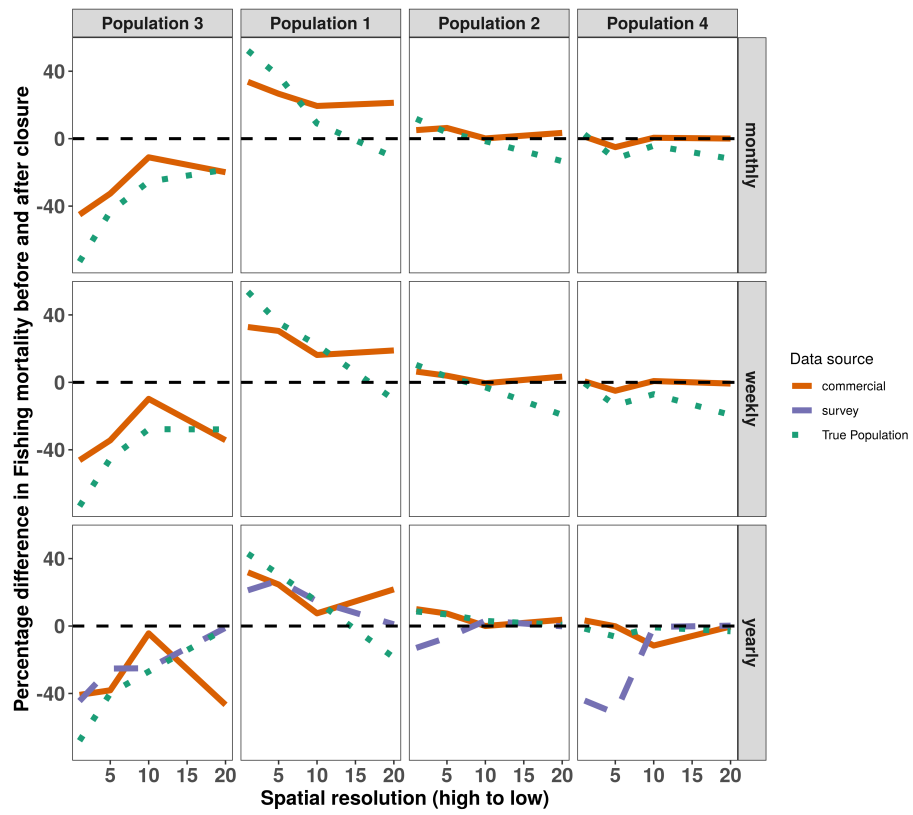


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

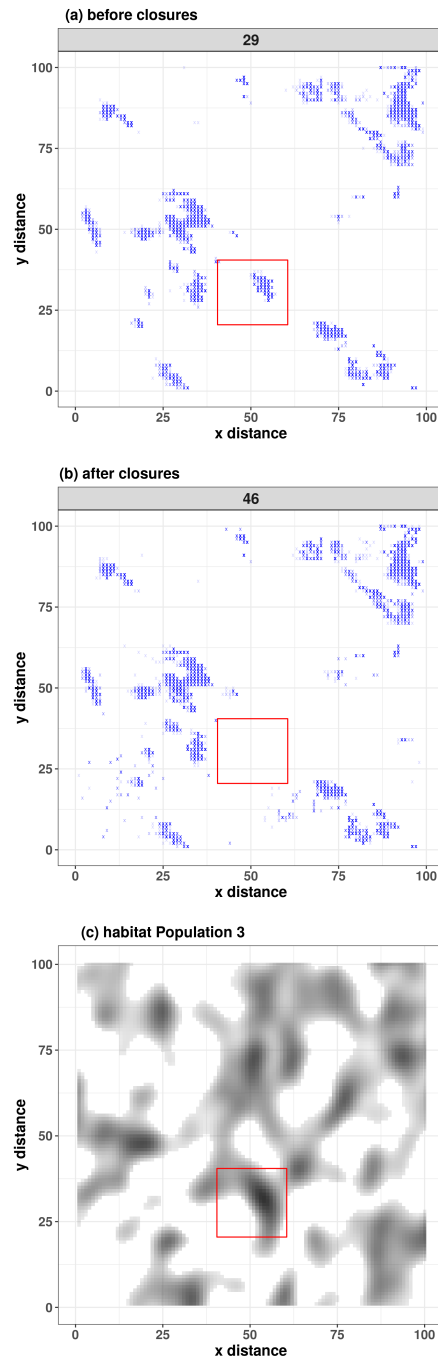


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

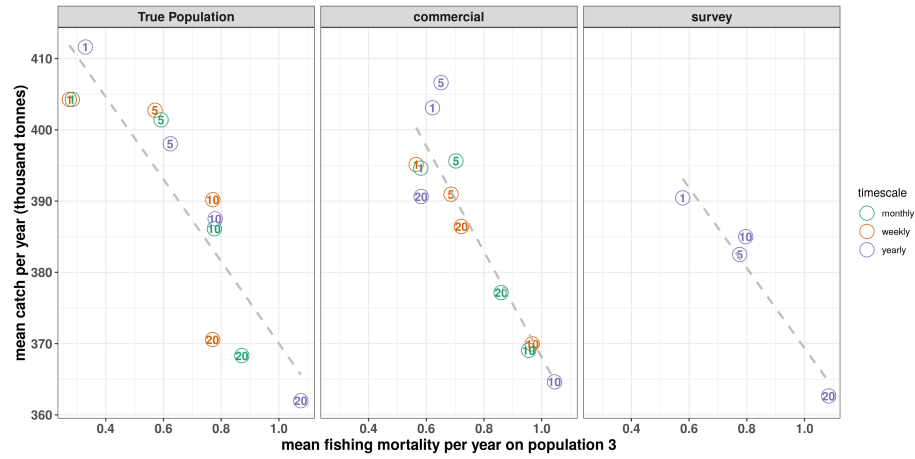


Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the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

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