

MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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Abstract

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

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

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

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

We simulated 50 years of fishing and used the results from the fisheries catch to draw inference on the underlying community structures. We compared this inference to a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying community structure. We i) used the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and ii) simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions to assess their effectiveness on reducing catches of a fish population.

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. We conclude from our simulations that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

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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. In doing so fisheries catch an assemblage of species and may discard over-quota catch when managed by single species quotas and fishers exhaust one or more

6 quota. This may lead to overexploitation of fish populations (Ulrich et al.,
7 2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the abil-
8 ity to maintain fishing mortality within sustainable limits (Alverson et al., 1994;
9 Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the
10 biological and economic sustainability of fisheries. As such, there is increasing
11 interest in technical solutions such as gear and spatial closures as measures to
12 reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill,
13 2008; Bellido et al., 2011; Cosgrove et al., 2019).

14
15 Adaptive spatial management strategies have been proposed as a way of
16 reducing discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014).
17 Implementation of avoidance measures is, however, restricted by lack of knowl-
18 edge of fish and fishery spatiotemporal dynamics and understanding of the scale
19 at which processes become important for management. Understanding the cor-
20 rect scale for spatial measures is crucial for implementing solutions at a reso-
21 lution that ensures effective management (Dunn et al., 2016) while minimising
22 economic impact. For example, the problem can be to identify a scale that
23 promotes species avoidance for vulnerable or low quota species while allowing
24 continuance of sustainable fisheries for available quota species.

25
26 Identifying appropriate scales for spatial fisheries management has been a
27 challenge in the past that has led to ineffectual measures with unintended conse-
28 quences. These unintended consequences limited impacts towards management
29 objectives, or increased benthic impact on previously unexploited areas (e.g.
30 the cod closure in the North Sea (Rijnsdorp et al., 2001; Dinmore et al., 2003)).
31 SENTENCE HERE ATTRIBUTING THE CHALLENGE OF IDENTIFYING
32 APPROPRIATE SCALES TO COURSE SPATIAL INFORMATION. More re-
33 fined spatial information has since become available through the combination of
34 logbook and Vessel Monitoring System (VMS) data (Lee et al., 2010; Bastardie
35 et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016) and more real-time spatial
36 management has been possible (e.g. Holmes et al., 2011). Such information is,

37 however, derived from an inherently biased sampling programme, targeted fish-
38 ing, where fishers establish favoured fishing grounds through an explore-exploit
39 strategy (Bailey et al., 2018) where they search for areas with high catches and
40 then use experience to return to areas where they’ve experienced high catch in
41 the past.

42

43 In order to understand the effect of spatiotemporal aggregation of data we
44 ask two fundamental questions regarding inference derived from observational
45 data:

- 46 1. How does sampling-derived data reflects the underlying community struc-
47 ture?
- 48 2. How does data aggregation and source impact on spatial fisheries man-
49 agement measures?

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

62

63 2. Materials and Methods

64 A simulation model that is modular and discrete-event based was developed.
65 This approach enables efficient computation by allowing for sub-modules imple-
66 mented on time-scales appropriate to capture the characteristic of the different
67 processes (Figure 1). The following sub-modules were included to capture the
68 full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population
69 movement, 4) fishery dynamics.

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

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

81 2.1. Population dynamics

82 The basic population level processes were simulated using a modified two-
83 stage Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dich-
84 mont et al., 2003) occurring at a daily time-step. A daily time-step was chosen
85 to discretise continuous population processes on a biologically relevant and com-
86 putationally tractable timescale. Population biomass growth and depletion for
87 pre-recruits and recruited fish were modelled separately as a function of previ-
88 ous recruited biomass, intrinsic population growth and recruitment functionally
89 linked to the adult population size. Biomass for each cell c was incremented

each day d as follows (the full parameter list is detailed in Table 1):

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

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

96

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

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

where $C_{c,d}$ is the summed catch from the fishing model across all fleets and vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass for the population in the cell. Here, catch and fishing mortality are the sum of those across all fleets and vessels, where $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot D_{c,d,p}$ with fl , v and p the fleet, vessel and population respectively and E and Q fishing effort and catchability of the gear, and D is the density of the population at the location fished.

108

2.2. Recruitment dynamics

Recruitment is modelled through a function relating the adult biomass to recruits at time of recruitment. In *MixFishSim*, it can be modelled either either

112 as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

113 Where α is the maximum recruitment rate, β the spawning stock biomass (SSB)
114 required to produce half the maximum stock size, S current stock size and σ^2
115 the variability in the recruitment due to stochastic processes, or a stochastic
116 Ricker form (Ricker, 1954):

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

117 where α is the maximum productivity per spawner and β the density dependent
118 reduction in productivity as the SSB increases. In our example application the
119 Beverton-Holt form of stock recruit relationship was used for all populations
120 though either functional form can be chosen.

121 2.3. Population movement dynamics

122 To simulate fish population distribution in space and time a Gaussian spatial
123 process was employed to model habitat suitability for each of the populations
124 on a 2d grid. JM: MENTION IN THE INTRODUCTION

125

126 We first defined a Gaussian random field process, $\{S(c) : c \in \mathbb{R}^2\}$, where
127 for any set of cells c_1, \dots, c_n , the joint distribution of $S = \{S(c_1), \dots, S(c_n)\}$
128 is multivariate Gaussian with a *Matérn* covariance structure, where the corre-
129 lation strength weakens with distance. This enables us to model the spatial
130 autocorrelation observed in animal populations where density is more similar
131 in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the
132 parameters to implement different spatial structures for the populations.

133

134 The habitat for each of the populations was generated with the *RFSimulate*
135 function of the *RandomFields* R package (Schlatter et al., 2015), that simulates a

136 Gaussian Random Field process given a user defined error model and correlation
 137 structure. We define a stationary habitat field and combine with a temporally
 138 dynamic thermal tolerance field to imitate two key drivers of population dy-
 139 namics. Each population was initialised at a single location, and subsequently
 140 moved according to a probabilistic distribution based on habitat suitability (rep-
 141 resented by the normalised values from the GRFs), temperature and distance
 142 from current cell:

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

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

147
 148 During pre-defined weeks of the year the habitat suitability is modified with
 149 user-defined spawning habitat locations, resulting in each population having
 150 concentrated areas where spawning takes place. In the simulations the popu-
 151 lations move towards these cells in the weeks prior to spawning, resulting in
 152 directional movement towards the spawning grounds.

153 JM: WHAT ABOUT INDIVIDUAL INTERACTIONS:w

154 An advection-diffusion process controls population movement, with a time-
 155 varying temperature covariate used to change the interaction between time and
 156 suitable habitat on a weekly time-step. Each population p was assigned a ther-
 157 mal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population
 158 temperature suitability is defined that:

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

159 Where $Tol_{c,p,wk}$ is the tolerance of population p for cell c in week wk , $T_{c,wk}$ is
 160 the temperature in the cell given the week and μ_p and σ_p^2 the mean and standard
 161 deviation of the population temperature tolerance.

162

163 The final process results in a population structure and movement pattern
 164 unique to each species, with population movement occurring on a weekly basis.
 165 The decision to model population movement on a weekly timescale was to reflect
 166 that fish tend to aggregate in species specific locations that have been observed
 167 to last around one to two weeks (Poos and Rijnsdorp, 2007b). Therefore this
 168 process approximated the demographic shifts in fish populations throughout a
 169 year with seasonal spawning patterns (e.g. Figure S5).

170 *2.4. Fleet dynamics*

171 The fleet dynamics can be broadly categorised into three components; fleet
 172 targeting - that determined the fleet catch efficiency and preference towards a
 173 particular species; trip-level decisions, that determined the initial location to
 174 be fished at the beginning of a trip; and within-trip decisions, that determined
 175 movement from one fishing spot to another within a trip. Together, these el-
 176 ements implemented an explore-exploit type strategy for individual vessels to
 177 maximise their catch from an unknown resource distribution Bailey et al. (2018).
 178 The decision to use an individual based model for fishing vessels was taken be-
 179 cause fishers are heterogeneous in their location choice behaviour due to different
 180 objectives, risk preference and targeting preference (Van Putten et al., 2012).
 181 Therefore in the simulations fleet dynamics are the productive of individual
 182 experiences rather than pre-defined group dynamics.

183 *2.4.1. Fleet targeting*

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

191 *2.4.2. Trip-level decisions*

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

202 *2.4.3. Within-trip decisions*

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

216
217 We use a *Lévy flight* which is a particular form of random walk charac-
218 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-
219 ceived a lot of attention in ecological theory in recent years as having shown to
220 have very similar characteristics as those observed by animals in nature, and

221 being a near optimum searching strategy for predators pursuing patchily dis-
222 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,
223 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a
224 stochastic search pattern similar to that observed with a lévy flight. However,
225 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),
226 with the contention that search patterns may be more simply characterised as
227 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the
228 characteristics of the prey field (Sims et al., 2012).

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

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

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

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

242 Where β_1 , β_2 and β_3 are parameters determining the shape of the step function

243 in its relation to revenue, so that, a step from $(x1, y1)$ to $(x2, y2)$ is defined by:

$$\begin{aligned}
 (x2, y2) = & x1 + StepL \cdot \cos\left(\frac{\pi \cdot Br}{180}\right), \\
 & y1 + StepL \cdot \sin\left(\frac{\pi \cdot Br}{180}\right) \\
 \text{with } & Br_{t-1} < 180, Br_t = 180 + \sim vm[(0, 360), k] \\
 & Br_{t-1} > 180, Br_t = 180 - \sim vm[(0, 360), k]
 \end{aligned} \tag{9}$$

244 where k the concentration parameter from the von Mises distribution that we
 245 correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where max_k
 246 is the maximum concentration value, k , and $RefRev$ is parametrised as for β_3
 247 in the step length function. A realised example of the step length and turning
 248 angle relationships to revenue can be seen at Figure S15.

249 2.4.4. Local population depletion

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

261 2.5. Fisheries independent survey

262 A fisheries-independent survey is simulated where fishing on a regular grid
 263 begins each year at the same time for a given number of stations (a fixed station
 264 survey design). Catches of the populations at each station are recorded but not
 265 removed from the population. This provides a fishery independent snapshot
 266 of the populations at a regular spatial intervals each year, similar to scientific

267 surveys undertaken by fisheries research agencies.

268

269 *2.6. Software: R-package development*

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

273

274 **3. Parameterisation**

275 *3.1. Population models*

276 We parametrised the simulation model for four populations with different
277 demographics; growth rates, natural mortality and recruitment functions (Ta-
278 ble 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3,
279 S4) were defined to be unique to each population resulting in differently weekly
280 distribution patterns (Figures S5-S7). In addition, each of the populations was
281 assumed to have two defined spawning areas that result in the populations mov-
282 ing towards these areas in pre-defined weeks (Figure S2) with population-specific
283 movement rates (Table 4). In such a configuration, the individual habitat pref-
284 erences and thermal tolerances result in different spatial habitat use for each
285 population (Figure S9) and consequently different seasonal exploitation patterns
286 (Fishing mortality in Figure S10).

287 *3.2. Fleet parametrisation*

288 The fleets were parametrised to reflect five different characteristic fisheries
289 with unique exploitation dynamics (Table 5). By setting different catchability
290 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
291 and hence spatial dynamics. The random walk process implies that within a
292 fleet different vessels have different spatial distributions based on individual
293 experience. The step function was parametrised dynamically within the simu-
294 lations as the maximum revenue obtainable was not known beforehand. This

was implemented so that vessels take smaller steps when fishing at a location that yields landings value in the top 90th percentile of the value experienced in that year so far (as defined per fleet in Table 5).

With increasing probability throughout the simulation, fishing locations were chosen based on experience of profitable catches built up in the same month from previous years and from the previous trip. 'Profitable' in this context was defined as the locations where the top 70 % of expected profit would be found given 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 parameters for all populations ($Q_p = 1$). This approximates a real world survey design with limited seasonal and spatial coverage.

3.4. Example research question

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

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

327

328 The following steps are undertaken to determine closures:

- 329 1. Extract data source
- 330 2. Aggregate according to desired spatial and temporal resolution
- 331 3. Interpolate across entire area at desired resolution using simple kriging
332 using the *interp* function from the R package *akima* (Akima, 2006). JM:
333 SEE COMMENT
- 334 4. Close area covering top 5 % of catch rates

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

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

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

342 4. Results

343 4.1. Simulation dynamics

It can be seen from a single vessels movements during a trip that the vessel exploits four different fishing grounds, three of them multiple times (Figure S11), while across several trips fishing grounds that are further apart are fished (Figure S12). These different locations relate to areas where the highest revenue were

experienced, as shown by Figure S13, where several trips for the vessel overlaid on the revenue field, i.e.

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

Vessels from the same fleet (and therefore targeting preference) exploit similar but slightly different fishing grounds depending on their own personal experience during the explore phase of the fishery (Figure S14), that is the result of the randomness in the correlated random walk step function, with distance moved during the exploitation phase and the direction stochastically related to the revenue experienced on the fishing ground (Figure S15).

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

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

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

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

369 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and
370 20 x 20 grid lose a significant amount of information about the spatial resolu-
371 tions for all data sources, and some differences between the survey, commercial
372 and 'real population' data emerge.

373

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

390 *4.3. How does data aggregation and source impact on spatial fisheries manage-* 391 *ment measures?*

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

397 The trend in fishing mortality for each species show that in most cases the
398 fishery closure was successful in reducing fishing mortality on the species of in-

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

A regression tree (using the R package REEMtree (Sela and Simonoff, 2012)) highlights that the factor most contributing to differences in fishing mortality before and after the closure was the population (72 % showing that the closures were effective for population 3), followed by data resolution (21 %), data type (7 %) with the least important factor the timescale (< 1 %). In general the finer the spatial resolution of the data used the greater reduction in fishing mortality for population 3 after the closures (Figure 5). The notable outliers are the commercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly timescale, where closures were nearly as effective as the fine-scale resolution. In this case the closures were sufficiently large to protect a core area of the habitat 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 S17) that may have consequences in terms of restricting the fishery in a much larger area than necessary.

5. Discussion

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

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

443

444 5.1. *Simulation dynamics*

445 We employ a simulation approach to model each of the population and fish-
 446 ery dynamics in a hypothetical 'mixed fishery', allowing us to i) evaluate the
 447 consequences of different aggregation assumptions on our understanding of the
 448 spatiotemporal distribution of the underlying fish populations, and ii) evaluate
 449 the effectiveness of a spatial closure given those assumptions.

450

451 Our approach is unique in that it captures fine scale population and fish-
 452 ery dynamics and their interaction in a way not usually possible with real data
 453 and thus not usually considered in fisheries simulations. While other simulation
 454 frameworks seek to model individual vessel dynamics based on inferred dynam-
 455 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
 456 identify measures to meet particular management goals (Bailey et al., 2018), our
 457 framework allows users to explore the assumptions in modelling observational

458 data and evaluate the underlying dynamics of such approaches at a fine spatial
459 and temporal scale. This offers the advantage that larger scale fishery patterns
460 are emergent properties of the system and results can be compared to those
461 obtained under a statistical modelling framework.

462

463 Typically, simulation models that treat fish as individuals are focussed on
464 exploring the inter- and intra- specific interactions among fish populations (e.g.
465 OSMOSE Shin et al. (2004)) in order to understand how they vary over space
466 and time. Our focus was on understanding the strengths and limitations of
467 inference from catch data obtained through commercial fishing activity with
468 fleets exploiting multiple fish populations and realising catch distributions that
469 may differ from the underlying populations. As such, we favoured a minimum
470 realistic model of the fish populations (Plagányi et al., 2014), while incorporating
471 detailed fishing dynamics that take account of different drivers in a mechanistic
472 way. In this way we take account of heterogeneity in fleet dynamics due to
473 different preferences and drivers similarly to other approaches (Fulton et al.,
474 2011), but at an individual vessel rather than fleet level. We do not explicitly
475 define fleets as rational profit maximisers at the outset, but consider there are
476 several stages to development of the fishery; information gathering through
477 search where the resource location is not known, followed by individual learnt
478 behaviour of profitable locations. This provides a realistic model of how fishing
479 patterns are established and maintained to exploit an uncertain resource through
480 an explore-exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

481 5.2. *How does sampling-derived data reflect the underlying population structure?*

482 Our results demonstrate the importance of considering data scale and resolu-
483 tion when using observational data to support management measures. We find
484 that understanding of the community composition dynamics will depend on the
485 level of data aggregation and its important to consider the scale of processes;
486 including population movement rates, habitat uniformity and fishing targeting
487 practices if potential biases in data are to be understood and taken into account.

488

489 Our simulation shows that, despite biases introduced through the fishing
 490 process, the commercially derived data could still inform on the key spatial
 491 patterns in the community structures where the fisheries occurred, which was
 492 spatially limited due to the “hotspots” of commercially valuable species be-
 493 ing fished. Similarly, despite the even spatial coverage the survey was able to
 494 capture some of the same spatial patterns as the ‘real population’, but missed
 495 others due to gaps between survey stations limiting spatial and temporal cov-
 496 erage. This provides a challenge when modelling unsampled areas in inferring
 497 species distribution maps, though these limitations may be overcome by un-
 498 derstanding the relationship between the species and habitat covariates where
 499 these are known at unsampled locations (Robinson et al., 2011).

500

501 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 502 *ment measures?*

503 From our simulations spatial disaggregation was more important than the
 504 temporal disaggregation of the commercial data. This reflects the fact that there
 505 was greater spatial heterogeneity over the spatial domain than experienced in
 506 individual locations over the course of the year (Figure S9). This indicates that
 507 fixed closures, at the right resolution, when based on commercially derived data
 508 have the potential to reduced fishing mortality. The likely cost of poor spatial
 509 and temporal resolution is associated with reduced effectiveness and potentially
 510 closing fishing opportunities for other fisheries.

511

512 Two contrasting real world approaches in this respect were the spatial clo-
 513 sures to protect cod in the North Sea. In one example, large scale spatial closures
 514 were implemented with little success due to effort displacement to previously
 515 unfished areas (Dinmore et al., 2003), while in another small scale targeted
 516 spatiotemporal closures were considered to have some effect in reducing cod
 517 mortality without having to disrupt other fisheries significantly (Needle and

518 Catarino, 2011). These examples emphasise the importance of considering the
519 right scale and aggregation of data when identifying area closures and the need
520 to consider changing dynamics in the fisheries in response to such closures.

521

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

527 *5.4. Model assumptions and caveats*

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

532

533 Fish populations in our simulations move in pre-defined timescales and ac-
534 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).
535 Our assumptions in parametrising the model (movement rates, temperature tol-
536 erances) will have a direct impact on our conclusions on the relative importance
537 of spatial and temporal processes. These assumptions could be explored in a
538 future study by varying the parameters and assessing the robustness of our con-
539 clusions. For our example application we have chosen movement rates to reflect
540 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

541

542 In addition, we have assumed that fishing vessels are not restricted by quota
543 and therefore discarding of species for which vessels have no quota or that are
544 unwanted is not taken into account. This is likely to be a significant source of
545 bias in any inference using commercial data and should also be explored. For
546 example, MixFishSim could be altered to allow for spatiotemporal appraisal of
547 the impact of discarding on fisher behaviour and underlying populations via in-

548 clusion as discarding behaviour, or through move-on rules or cessation of fishing
549 activity when quota is exhausted.

550

551 5.5. *Future applications of MixFishSim*

552 We consider that the increased availability of high resolution catch and lo-
553 cational information from commercial fisheries will require it to be a key source
554 of data for ensuring management is implemented at the right scale in future.
555 For example, identifying hot-spots for bycatch reduction or identifying spatial
556 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
557 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
558 potential to test some of the assumptions behind the modelling approaches in
559 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
560 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
561 els under different data generation processes as exemplified by Stock et al. (2019)).

562

563 Other novel applications of our framework could be; testing different sur-
564 vey designs given multiple species and data generating assumptions (Xu et al.,
565 2015); commercial index standardisation methods and approaches and under-
566 standing of appropriate scales and data aggregations and non-proportionality
567 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
568 exploring assumptions about the distribution of natural mortality and fishing
569 mortality throughout the year and importance of capturing in-year dynamics
570 in estimating stock status (Liu and Heino, 2013); at sea sampling scheme de-
571 signs to deliver unbiased estimates of population parameters Cotter and Pilling
572 (2007); Kimura and Somerton (2006); adaptive management (Walters, 2007;
573 Dunn et al., 2016); testing the ability of commonly employed fleet dynamics
574 models such as Random Utility Models to capture fine scale dynamics and un-
575 derstand their importance Girardin et al. (2016); and as a detailed operating
576 model in a management strategy evaluation Mahévas and Pelletier (2004).

577

578 6. Conclusions

579 MixFishSim provides a detailed simulation framework to explore the inter-
580 action of multiple fisheries exploiting different fish populations. The framework
581 enables users to evaluate assumptions in modelling commercially derived data
582 through comparison to the true underlying dynamics at a fine spatial and tem-
583 poral scale. Understanding these dynamics, the limitations of the data and any
584 potential biases that may be introduced when making inference on spatiotempo-
585 ral interactions will enable users to identify weaknesses in modelling approaches
586 and identify where data collection is needed to strengthen inference.

587
588 Our application shows that inference on community dynamics may change
589 depending on the scale of data aggregation. There is an important balance in
590 ensuring that the data are sufficiently spatially and temporally disaggregated
591 that the main features of the data are captured, yet maintaining enough data
592 coverage that the features can be distinguished. We found in our application
593 that there was greater spatial heterogeneity than temporal heterogeneity and
594 that when using aggregated data to define spatial closures coarser temporal reso-
595 lution (months instead of weeks) could still achieve the same results in reducing
596 exploitation rates of a vulnerable species at the highest temporal resolution
597 data. Conversely, reducing the spatial resolution had a negative effect on the
598 effectiveness of the measures (though importantly, there was still some benefit
599 even with coarse spatial resolution).

600
601 While any findings are likely to be case specific, our findings emphasise the
602 need to understand population demographics, habitat use and movement rates
603 in designing any closure scenario based on observational sampling. This infor-
604 mation can then be used to set the bounds on data aggregation used in modelling
605 studies aimed at informing the management measures.

606
607 MixFishSim has numerous potential additional applications as it enables

608 the user to apply methods to a fisheries system where there is detailed under-
609 standing of underlying spatiotemporal dynamics. This enables identification of
610 weaknesses or limitations which would not be possible otherwise. In future, we
611 recommend use of the framework to test hypothesis that are otherwise unable
612 to be analysed using real world data due to limitations of data collection. That
613 way the knowledge gained through simulation can inform the future design of
614 management measures.

615 **Abbreviations**

616 Detail any unusual ones used.

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623 **Appendices**

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

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}
$S_{c,d}$	is the stock size in cell c for day d	d^{-1}
α	the maximum recruitment rate	kg
β	the stock size required to produce half the maximum rate of recruitment	kg

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

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

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

Variable	Meaning	Units
Short-term fleet dynamics		
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg ⁻¹
StepL	Step length for vessel	euclidean distance
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 setting

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	10	10	10
Movement λ	0.1	0.1	0.1	0.1
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	6	27	18	0.3
Beverton-Holt Recruit 'b'	4	4	11	0.5
Beverton-Holt Recruit 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	0.3	0.3	0.3
wt	1	1	1	1
wt_{d-1}	0.1	0.1	0.1	0.1
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ	12	15	17	14
σ^2	8	9	7	10

Table 5: Fleet dynamics parameter setting

Parameter	Fleet	Fleet	Fleet	Fleet	Fleet
	1	2	3	4	5
Targeting preferences	pop	pop	-	pop 4	pop
	2/4	1/3			2/3
Price Pop1	100	100	100	100	100
Price Pop2	200	200	200	200	200
Price Pop3	350	350	350	350	350
Price Pop4	600	600	600	600	600
Q Pop1	0.01	0.02	0.02	0.01	0.01
Q Pop2	0.02	0.01	0.02	0.01	0.03
Q Pop3	0.01	0.02	0.02	0.01	0.02
Q Pop4	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_3	Q90	Q90	Q85	Q90	Q80
step function $rate$	20	30	25	35	20
Past Knowledge	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios. Results show the fishing mortality before the closure (f.before) and after the closure (f.after) and the percentage change in f (f.change). The results are ordered by most effective scenario first, least effective last.)

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

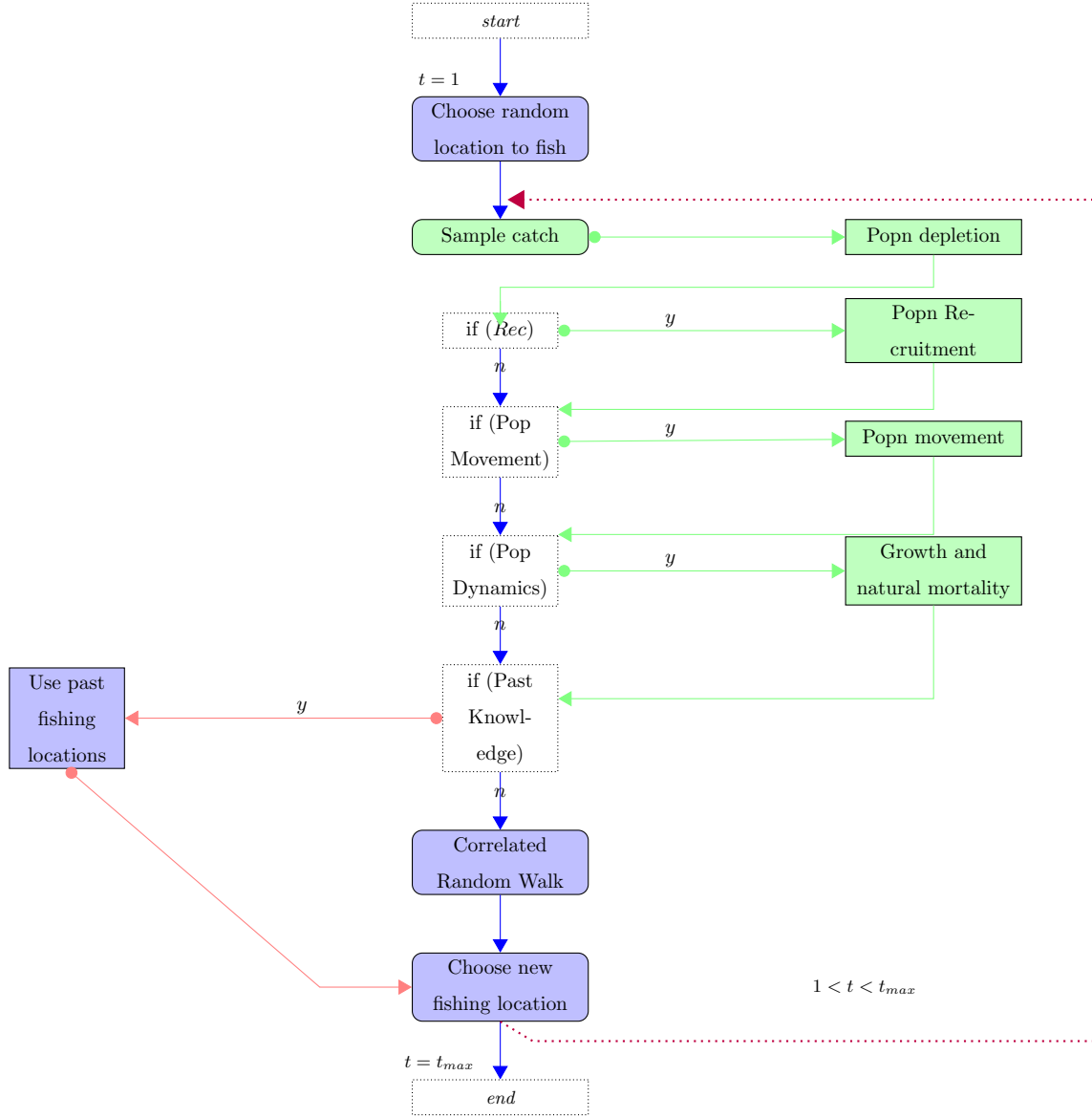


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics) logic gates for recruitment periods, population movement and population dynamics for each of the populations, (Past Knowledge) a switch whether to use a random (exploratory) or past knowledge (exploitation) fishing strategy.

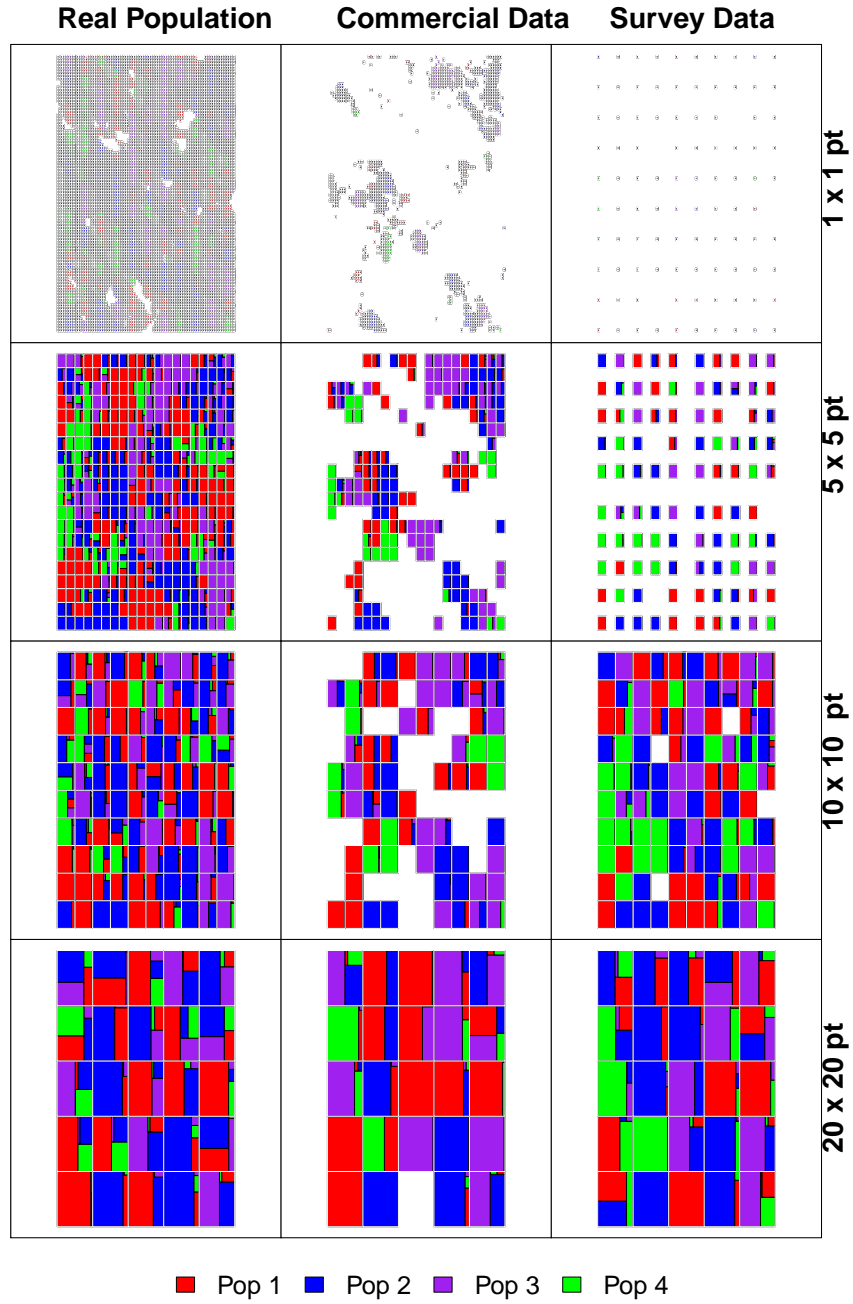


Figure 2: Data aggregation at different spatial resolutions over a ten year period

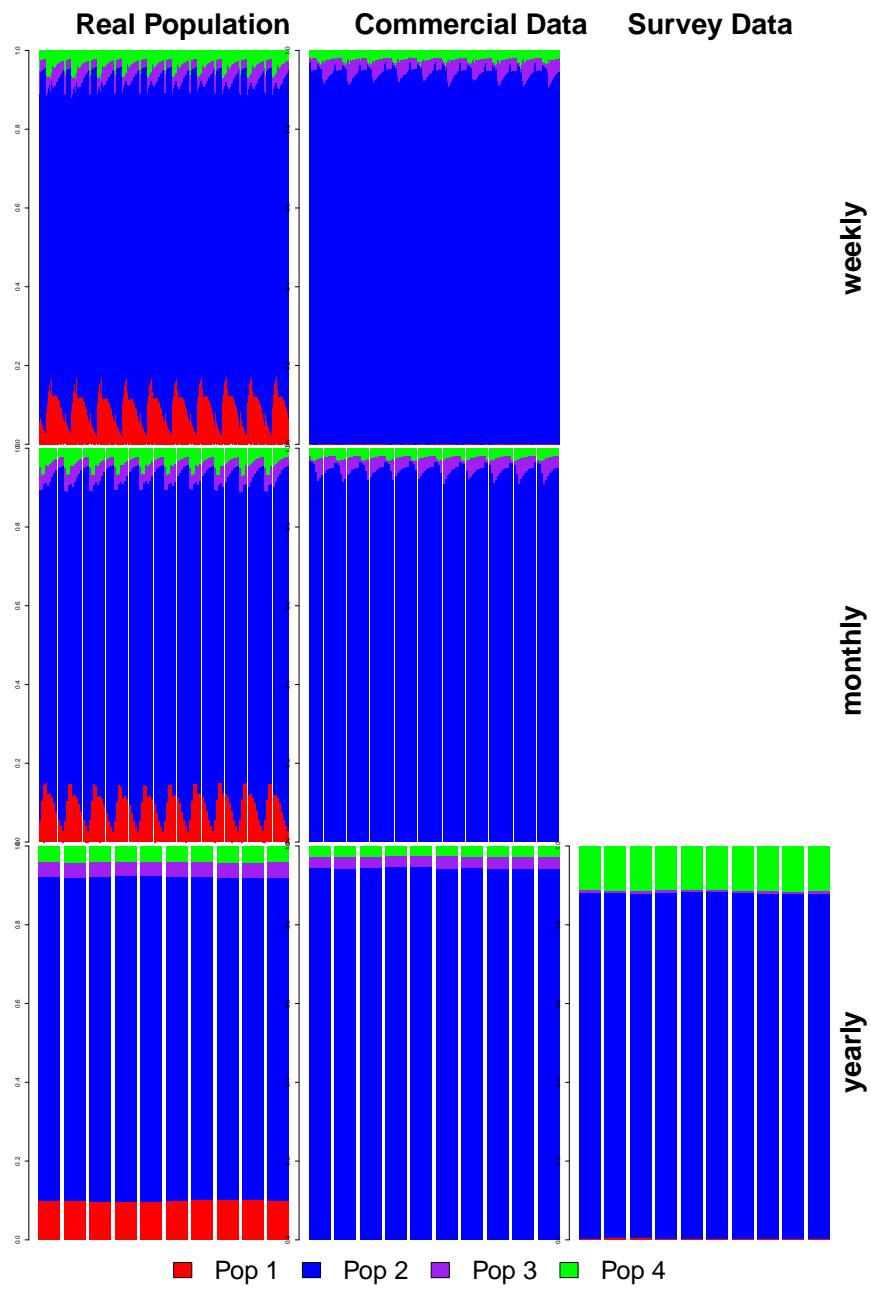


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

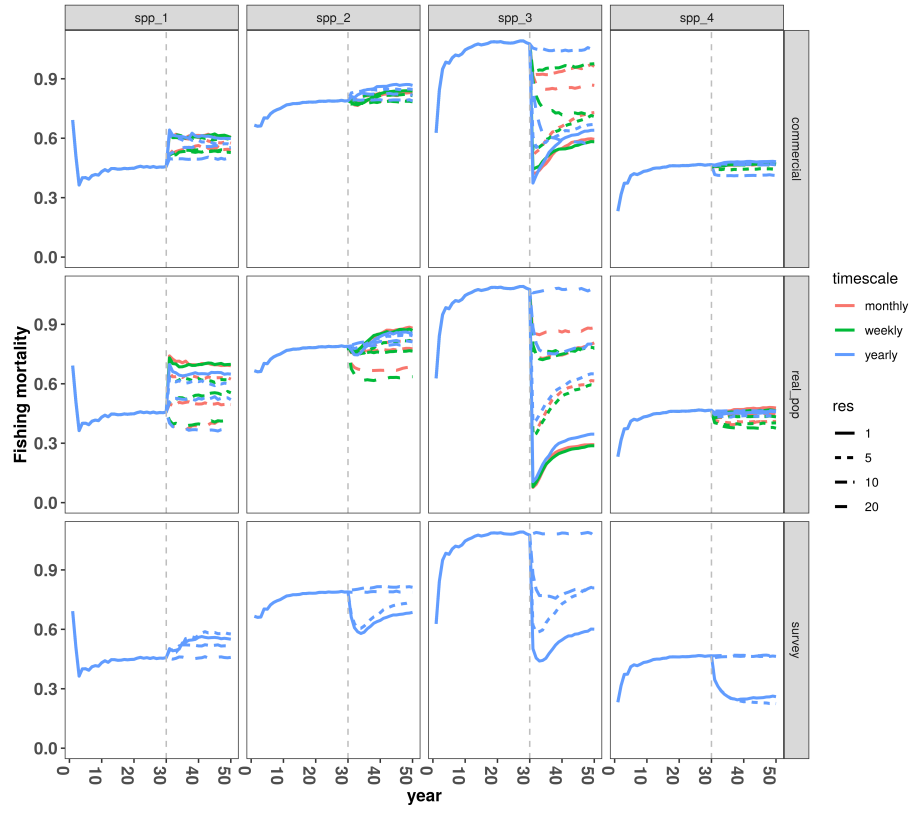


Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

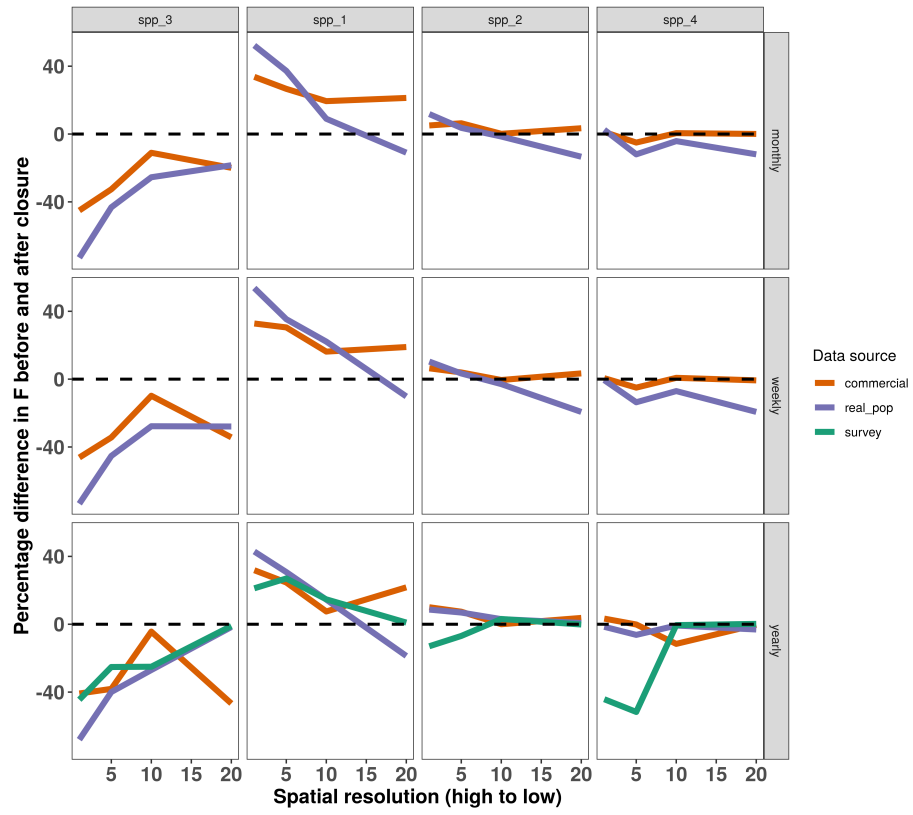


Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

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