

Working title: 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 event-based simulation model incorporating: i) delay-difference population dynamics, ii) population movement 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. 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 was simulated and used to draw inference on the underlying community structures. We compared inferences based on: commercial catch, a simulated fixed-site sampling survey design and the true underlying community. We i) establish the potential limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and then ii) simulated an area closure based on 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. We conclude from our example framework appli-

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cation that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale. [NEED A LITTLE MORE DETAIL OF THE RESULTS HERE - 2 MORE SENTENCES ON KEY TAKE-HOME RESULTS]

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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 in ‘mixed fisheries’ this can result in catch of low quota or protected species. This leads to discarding of over-quota catch if it is a species for which they have no quota, limiting control over 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; Batsleer et al., 2015).

10

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Reville, 2008; Bellido et al., 2011; Cosgrove et al., 2019) and adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2014; 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. Implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management.

21

Understanding the correct scale for spatial measures is also crucial as it

23 enables implementation of effective solutions which minimise economic impact
24 (Dunn et al., 2016). For example, the problem can be to identify a scale that
25 promotes species avoidance for vulnerable or low quota species while allowing
26 continuance of sustainable fisheries for available quota species. Identifying the
27 correct spatial scale remains a challenge because data on fish location at high
28 temporal and spatial resolutions is expensive and difficult to collect and proxies
29 are usually inferred from scientific surveys or commercial catches with limited
30 spatial and temporal resolution.

31
32 Identifying appropriate spatial scales for fisheries closures has been a identi-
33 fied as crucial to their success (Costello et al., 2010; Dunn et al., 2016). Inference
34 is hampered where spatial information is coarse due to low resolution report-
35 ing of fisheries catch which is aggregated across larger gridded areas (Branch
36 et al., 2005). Further, if data does not allow identification of spatial features
37 it may lead to poorly sited closures which are ineffectual or have unintended
38 consequences. For example, increased benthic impact on previously unexploited
39 areas from the cod closure in the North Sea were observed without the intended
40 effect of reducing cod exploitation (Rijnsdorp et al., 2001; Dinmore et al., 2003)).
41 More refined spatiotemporal information has since become available through the
42 combination of logbook and Vessel Monitoring System (VMS) data (Lee et al.,
43 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016) and
44 more real-time spatial management has been possible (e.g. Holmes et al., 2011).
45 However, fishers establish favoured fishing grounds through an explore-exploit
46 strategy (Bailey et al., 2018) where they search for areas with high catches and
47 then use experience to return to areas where they’ve experienced high catch in
48 the past. This leads to an inherently biased sampling where target species are
49 over-represented in the catch as fishers exploit areas of high abundance.

50
51 To understand the effect of spatiotemporal aggregation of data and fishery
52 targeting we ask two fundamental questions regarding inference derived from
53 observational data:

54 1. How does sampling-derived fisheries data reflects the underlying commu-
55 nity structure?

56 2. How does data aggregation and source impact on spatial fisheries man-
57 agement measures?

58 To answer these questions we i) develop a simulation model where popula-
59 tion dynamics are highly-resolved in space and time by use of a Gaussian spatial
60 process to define suitable habitat for different populations. Precise locations of
61 the fish being known directly rather than inferred from sampling or commercial
62 catch, we can use the population model to validate how inference from fisheries-
63 dependent and fisheries independent sampling relates to the real community
64 structure in a way we could not with real data. We ii) compare, at different
65 spatial and temporal aggregations, the real (simulated) population distributions
66 to samples from fisheries-dependent and fisheries independent catches to test if
67 these are a true reflection of the relative density of the populations. We then
68 iii) simulate a fishery closure to protect a species based on different spatial and
69 temporal data aggregations.

70

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

73 2. Materials and Methods

74 An event-based simulation model of a hypothetical fishery was developed as
75 a software package (*MixFishSim*). The modular approach enabled efficient com-
76 putation by allowing for sub-modules implemented on time-scales appropriate
77 to capture the characteristic of the different processes (Figure 1). The following
78 sub-modules were included to capture the full system: 1) Population dynamics,
79 2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

80

Population dynamics operate on a daily time-step, while population movement occurs on a weekly time-step, with the fishing module operating on a tow-by-tow basis (i.e. multiple events a day).

2.1. Population dynamics

The basic population level processes were simulated using a modified two-stage Deriso-Schnute delay difference model which models the fish populations in terms of aggregate biomass of recruits and mature components rather than keeping track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A daily time-step was chosen to discretise continuous population processes on a biologically relevant and computationally tractable timescale. Population biomass growth was modelled as a function of previous recruited biomass, intrinsic population growth and recruitment functionally 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 .

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 $F_{c,d}$:

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

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.

112

113 2.2. Recruitment dynamics

Recruitment is modelled through a function relating to adult biomass. In *MixFishSim*, it can be either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

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

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

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases.

123 2.3. Population movement dynamics

Population movement is a combination of random (diffusive) movement, governed by a stochastic process where movement between adjacent cells is described by a set of probabilities, and directed (advective) movement where at certain times of year the population moves towards spawning grounds by

128 increasing the probabilities of moving into the spawning grounds from adjacent
 129 cells. We characterise a set of different fishing fleet dynamics exploiting four
 130 fish populations with different spatial and population demographics.

131

132 To simulate fish population distribution in space and time a Gaussian spa-
 133 tial process was employed to model habitat suitability for each of the popula-
 134 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
 135 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
 136 $\{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,
 137 where the correlation strength weakens with distance. This enables us to model
 138 the spatial autocorrelation observed in animal populations where density is more
 139 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we
 140 change the parameters to implement different spatial structures for the differ-
 141 ent populations using the *RandomFields* R package (Schlatter et al., 2015). We
 142 define a stationary habitat field and combine with a temporally dynamic ther-
 143 mal tolerance field to imitate two key drivers of population dynamics. Each
 144 population was initialised at a single location, and subsequently moved accord-
 145 ing to a probabilistic distribution based on habitat suitability (represented by
 146 the normalised values from the GRFs), temperature and distance from current
 147 cell:

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

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

152

153 During pre-defined weeks of the year the habitat suitability is modified with
 154 user-defined spawning habitat locations, resulting in each population having
 155 concentrated areas where spawning takes place. In the simulations the popu-
 156 lations move towards these cells in the weeks prior to spawning, resulting in

157 directional movement towards the spawning grounds.

158

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

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

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

167

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

175 2.4. Fleet dynamics

176 Fleet dynamics can be broadly categorised into three components: fleet tar-
177 geting - that determined the fleet catch efficiency and preference towards a
178 particular species; trip-level decisions, that determines the initial location to
179 be fished at the beginning of a trip; and within-trip decisions, that determines
180 movement from one fishing spot to another within a trip. Together, these ele-
181 ments implement an explore-exploit type strategy for individual vessels to max-
182 imise their catch from an unknown resource distribution (Bailey et al., 2018).
183 The decision to use an individual based model for fishing vessels was taken

184 because fishers are heterogeneous in their location choice behaviour due to dif-
 185 ferent objectives, risk preference and targeting preference (Van Putten et al.,
 186 2012). Therefore in the simulations fleet dynamics reflect individual experiences
 187 rather than pre-defined group dynamics.

188 2.4.1. Fleet targeting

189 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
 190 and a population specific efficiency, $Q_{fl,p}$. Thus, the product of these parame-
 191 ters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential
 192 targeting of one population over another. This, in combination with the param-
 193 eter choice for the step-function defined below (as well as some randomness from
 194 the exploratory fishing process) determined the preference of fishing locations
 195 for the fleet.

196 2.4.2. Trip-level decisions

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

207 2.4.3. Within-trip decisions

208 Fishing locations within a trip are initially determined by a modified ran-
 209 dom walk process. As the simulation progresses the within-trip decision become
 210 gradually more influenced by experience gained from past fishing locations (as
 211 per the initial trip-level location choice), moving location choice towards areas
 212 of higher perceived profit. A random walk was chosen for the exploratory fishing

213 process as it is the simplest assumption commonly used in ecology to describe
 214 optimal animal search strategy for exploiting heterogeneously distributed prey
 215 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-
 216 dom walk, movement is a stochastic process through a series of steps. These
 217 steps have a length, and a direction that can either be equal in length or take
 218 some other functional form. The direction of the random walk was also cor-
 219 related (known as ‘persistence’) providing some overall directional movement
 220 (Codling et al., 2008).

221
 222 For our implementation of a random walk directional change is based on a
 223 negatively correlated circular distribution where a favourable fishing ground is
 224 likely to be “fished back over” by the vessel returning in the direction it came
 225 from. The step length (i.e. the distance travelled from the current to the next
 226 fishing location) is determined by relating recent fishing success, measured as
 227 the summed value of fish caught (revenue, Rev);

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

228 where L_p is landings of a population p , and Pr_p price of a population. All
 229 species prices were kept the same across fleets and seasons. Here, when fishing
 230 is successful vessels remain in a similar location and continue to exploit the local
 231 fishing grounds. When unsuccessful, they move some distance away from the
 232 current fishing location. The movement distance retains some degree of stochas-
 233 ticity, that can be controlled separately, but is determined by the relationship:

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

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

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

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

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

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

237 where L is the step length, k the concentration parameter from the von Mises
 238 distribution that we correlate with the revenue so that $k = (Rev + 1 / RefRev) *$
 239 max_k , where max_k is the maximum concentration value, k , and $RefRev$ is
 240 parametrised as for β_3 in the step length function. A realised example of the
 241 step length and turning angle relationships to revenue can be seen at Figure
 242 S12.

243 2.4.4. Local population depletion

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

253 2.5. Fisheries independent survey

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

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

261

262 2.6. Software: R-package development

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

266

267 3. Parameterisation

268 We parameterise *MixFishSim* to investigate the influence of data aggregation
269 on spatial inference.

270 3.1. Population models

271 We parametrised the simulation model for four example populations with
272 different demographics, growth rates, natural mortality and recruitment pa-
273 rameters (Table 4). Habitat preference (Figure S1) and temperature tolerances
274 (Figures S3, S4) were defined to be unique to each population resulting in dif-
275 ferently weekly distribution patterns (Figures S5-S7). In addition, each of the
276 populations was assumed to have two defined spawning areas that result in the
277 populations moving towards these areas in pre-defined weeks (Figure S2) with
278 population-specific movement rates (Table 4). In such a configuration, the in-
279 dividual habitat preferences and thermal tolerances result in different spatial
280 habitat use for each population (Figure 2) and consequently different seasonal
281 exploitation patterns (Fishing mortality in Figure 3).

282 3.2. Fleet parametrisation

283 The fleets were parametrised to reflect five different characteristic fisheries
284 with unique exploitation dynamics (Table 5). By setting different catchability
285 parameters ($Q_{fl,p}$) 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 parametrised dynamically within the simulations as the maximum revenue obtainable was not known beforehand. This was implemented so that vessels take smaller steps when fishing at a location that yields landings value in the top 90th percentile of the value experienced in that year so far (as defined per fleet in Table 5).

With increasing probability throughout the simulation, fishing locations were chosen based on experience of profitable catches built up in the same month from previous years and from the previous trip. 'Profitable' in this context was defined as the locations where the top 70 % of expected profit would be found given 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

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

318

319 *How does sampling-derived fisheries data reflect the underlying population*
320 *structure?*

321

322 To answer this question we compare different spatial and temporal aggrega-
323 tions of the real population distributions to:

324 a) **fisheries-independent data:** the inferred population from a fixed-site
325 sampling survey design as commonly used for fisheries monitoring pur-
326 poses;

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

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

333

334 The following steps are undertaken to determine closures:

- 335 1. Extract data source (real population, commercial or survey),
- 336 2. Aggregate according to desired spatial and temporal resolution,
- 337 3. Interpolate across entire area at desired resolution using simple bivariate
338 interpolation using the *interp* function from the R package *akima* (Akima,
339 2006). This is intended to represent a naive spatial model of catch rates,
340 without knowledge of the spatial population dynamics.
- 341 4. Close area covering top 5 % of catch rates

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

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

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

349 4. Results

350 4.1. Emergent 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 S9), while across several trips fishing grounds that are further apart are fished (Figure S10). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 4, where several trips for the vessel overlaid on the revenue field, i.e.

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

351 Vessels from the same fleet (and therefore targeting preference) may exploit
352 some shared and some different fishing grounds depending on their own personal
353 experience during the exploratory phase of the fishery (Figure S11). This results
354 from the randomness in the correlated random walk step function, with distance
355 moved during the exploitation phase and the direction stochastically related to
356 the revenue experienced on the fishing ground (Figure S12).

357 4.2. How does sampling-derived fisheries data reflect the underlying population 358 structure?

359 Figure 5 shows the aggregated catch composition from each of the data
360 sources over a ten-year period (to average seasonal patterns) at different spa-
361 tial 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 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the spatial resolutions for all data sources, and some differences between the survey, commercial and real population data emerge.

Figure 6 shows the consequences of different temporal aggregations of the data over a ten-year period, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area. In the real population, the monthly aggregation captures the major patterns of composition seen in the weekly data with the percentage of different species in the catch having similar mean and standard deviations. In the weekly data species 1 = 9.36 (3.99), species 2 = 83.2 (5.60), species 3 = 3.57 (1.23), species 4 = 3.91 (1.59); in the monthly data species 1 = 9.23 (3.87), species 2 = 83.3 (5.52), species 3 = 3.62 (1.15), species 4 = 3.86 (1.52). While means were similar some of the variation was lost when aggregated to an annual level; species 1 = 9.90 (0.173), species 2 = 82.2 (0.308), species 3 = 3.82 (0.119), species 4 = 4.03 (0.0502).

The commercial data on a weekly basis shows some of the same patterns as the real population, though the species 1 (in red) is less well represented and some weeks are missing catches from the area. Here, weekly and monthly compositions were nearly identical, with monthly composition of species 1 = 0.0472 (0.0139), species 2 = 94.4 (1.47), species 3 = 3.12 (1.47), species 4 =

2.40 (0.444). 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; species 1 = 0.372 (0.00473), species 2 = 87.7 (0.193), species 3 = 0.729 (0.0200), species 4 = 11.2 (0.172).

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 species 3, given availability of data and its use at different resolutions in order to evaluate the trade-offs in data sources.

The trend in fishing mortality for each species show that in most cases the fishery closure was successful in reducing fishing mortality on the species of interest (species 3; Figure 7), 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 8). 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 9) that may have consequences in terms of restricting the fishery in a much larger area than necessary.

5. Discussion

Our study presents a new highly resolved fisheries simulation framework, evaluates the importance of data scaling and considers potential bias introduced through data aggregation when using fisheries data to infer spatiotemporal dynamics of fish populations. Understanding how fishers exploit multiple heterogeneously distributed fish populations with different catch limits or conservation status requires detailed understanding of the overlap of resources; this is difficult to achieve using conventional modelling approaches due to species targeting in fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Often data are aggregated or extrapolated which requires assumptions about the spatial and temporal scale of processes. Our study explores the assumptions behind such aggregation and preferential sampling to identify potential impacts on management advice. With modern management approaches increasingly employing more nuanced spatiotemporal approaches to maximise productivity while taking account of both the biological and human processes operating on different time-frames (Dunn et al., 2016), understanding assumptions behind the data used - increasingly a combination of logbook and positional information from vessel monitoring systems - is vital to ensure measures are effective.

452

453 5.1. *Simulation dynamics*

454 We employ a simulation approach to model each of the population and fish-
455 ery dynamics in a hypothetical ‘mixed fishery’, allowing us to i) evaluate the
456 consequences of different aggregation assumptions on our understanding of the
457 spatiotemporal distribution of the underlying fish populations, and ii) evaluate
458 the effectiveness of a spatial closure given those assumptions.

459

460 Our approach is unique in that it captures fine scale population and fish-
461 ery dynamics and their interaction in a way not usually possible with real data
462 and thus not usually considered in fisheries simulations. While other simulation
463 frameworks seek to model individual vessel dynamics based on inferred dynam-
464 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
465 identify measures to meet particular management goals (Bailey et al., 2018), our
466 framework allows users to explore the assumptions in modelling observational
467 data and evaluate the underlying dynamics of such approaches at a fine spatial
468 and temporal scale. This offers the advantage that larger scale fishery patterns
469 are emergent properties of the system and results can be compared to those
470 obtained under a statistical modelling framework.

471

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

482

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

490

491 We take account of heterogeneity in fleet dynamics due to different prefer-
 492 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an
 493 individual vessel rather than fleet level. We do not explicitly define fleets as
 494 rational profit maximisers at the outset, but consider there are several stages
 495 to development of the fishery; information gathering through search where the
 496 resource location is not known, followed by individual learnt behaviour of prof-
 497 itable locations. This provides a realistic model of how fishing patterns are
 498 established and maintained to exploit an uncertain resource through an explore-
 499 exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

500 5.2. *How does sampling-derived fisheries data reflect the underlying population* 501 *structure?*

502 Our results demonstrate the importance of considering data scale and resolu-
 503 tion when using observational data to support management measures. We find
 504 that understanding of the community composition dynamics will depend on the
 505 level of data aggregation and its important to consider the scale of processes;
 506 including population movement rates, habitat uniformity and fishing targeting
 507 practices if potential biases in data are to be understood and taken into account
 508 (Figures X,Y,Z).

509

510 Our simulation shows that, despite biases introduced through the fishing
 511 process, the commercially derived data could still inform on the key spatial

512 patterns in the community structures where the fisheries occurred, which was
 513 spatially limited due to the “hotspots” of commercially valuable species being
 514 fished. Similarly, despite the even spatial coverage the survey was able to cap-
 515 ture some of the same spatial patterns as the real population, but missed others
 516 due to gaps between survey stations limiting spatial and temporal coverage
 517 (Figures X,Y,Z). This provides a challenge when modelling unsampled areas in
 518 inferring species distribution maps, though these limitations may be overcome
 519 by understanding the relationship between the species and habitat covariates
 520 where these are known at unsampled locations (Robinson et al., 2011).

521

522 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 523 *ment measures?*

524 From our simulations spatial disaggregation was more important than the
 525 temporal disaggregation of the commercial data. This reflects the fact that there
 526 was greater spatial heterogeneity over the spatial domain than experienced in
 527 individual locations over the course of the year (Figure 2).

528

529 The yearly data assumes the same proportion of each population caught at
 530 any time of the year due to the data aggregation. This assumption introduces
 531 ‘aggregation bias’ as the data may only be representative of some point (or no
 532 point) in time. The monthly data shows some consistency between the real
 533 population and commercial data for species 2 - 4, though species 1 remains
 534 under-represented. On an annual basis, interestingly the commercial data un-
 535 der represents the first species (in red) while the survey over represents species
 536 1. This is likely due to the biases in commercial sampling, with the fisheries
 537 not targeting the areas where species 1 are present and the survey sampling
 538 areas where species 1 is more abundant than on average. This indicates that
 539 fixed closures, at the right resolution, when based on commercially derived data
 540 have the potential to reduced fishing mortality. The likely cost of poor spatial
 541 and temporal resolution is associated with reduced effectiveness and potentially

542 closing fishing opportunities for other fisheries.

543

544 Two contrasting real world approaches in this respect were the spatial clo-
545 sures to protect cod in the North Sea. In one example, large scale spatial closures
546 were implemented with little success due to effort displacement to previously
547 unfished areas (Dinmore et al., 2003), while in another small scale targeted
548 spatiotemporal closures were considered to have some effect in reducing cod
549 mortality without having to disrupt other fisheries significantly (Needle and
550 Catarino, 2011). These examples emphasise the importance of considering the
551 right scale and aggregation of data when identifying area closures and the need
552 to consider changing dynamics in the fisheries in response to such closures.

553

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

559 *5.4. Model assumptions and caveats*

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

564

565 Fish populations in our simulations move in pre-defined timescales and ac-
566 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).
567 Our assumptions in parameterising the model (movement rates, temperature
568 tolerances) will have a direct impact on our conclusions on the relative impor-
569 tance of spatial and temporal processes. These assumptions could be explored
570 in a future study by varying the parameters and assessing the robustness of our
571 conclusions. For our example application we have chosen movement rates to re-

572 fleet aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

573

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

582

583 5.5. Future applications of *MixFishSim*

584 We consider that the increased availability of high resolution catch and lo-
585 cational information from commercial fisheries will require it to be a key source
586 of data for ensuring management is implemented at the right scale in future.
587 For example, identifying hot-spots for bycatch reduction or identifying spatial
588 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
589 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
590 potential to test some of the assumptions behind the modelling approaches in
591 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
592 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
593 els under different data generation processes as exemplified by Stock et al. (2019)).

594

595 Other novel applications of our framework could be: testing different sur-
596 vey designs given multiple species and data generating assumptions (Xu et al.,
597 2015); commercial index standardisation methods and approaches and under-
598 standing of appropriate scales and data aggregations and non-proportionality
599 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
600 exploring assumptions about the distribution of natural mortality and fishing
601 mortality throughout the year and importance of capturing in-year dynamics

in estimating stock status (Liu and Heino, 2013); 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., 2016); and as a detailed operating model in a management strategy evaluation (Mahévas and Pelletier, 2004).

6. Conclusions

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

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

631 even with coarse spatial resolution).

632

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

638

639 *MixFishSim* has numerous potential additional applications as it enables
640 the user to apply methods to a fisheries system where there is detailed under-
641 standing of underlying spatiotemporal dynamics. This enables identification of
642 weaknesses or limitations which would not be possible otherwise. In future, we
643 recommend use of the framework to test hypothesis that are otherwise unable
644 to be analysed using real world data due to limitations of data collection. That
645 way the knowledge gained through simulation can inform the future design of
646 management measures.

647 **Abbreviations**

648 Detail any unusual ones used.

649 **Acknowledgements**

650 those providing help during the research..

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655 **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

Table 7: Proportions of each species at different levels of temporal aggregation

data_type	timescale	spp1	sd_spp1	spp2	sd_spp2	spp3	sd_spp3	spp4	sd_spp4
commercial	monthly	0.047	0.014	94.435	1.470	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
real_pop	monthly	9.225	3.872	83.287	5.522	3.624	1.151	3.864	1.519
real_pop	weekly	9.358	3.992	83.165	5.596	3.567	1.233	3.910	1.592
real_pop	yearly	9.899	0.173	82.250	0.308	3.821	0.119	4.031	0.050
survey	yearly	0.372	0.005	87.667	0.193	0.729	0.020	11.232	0.172

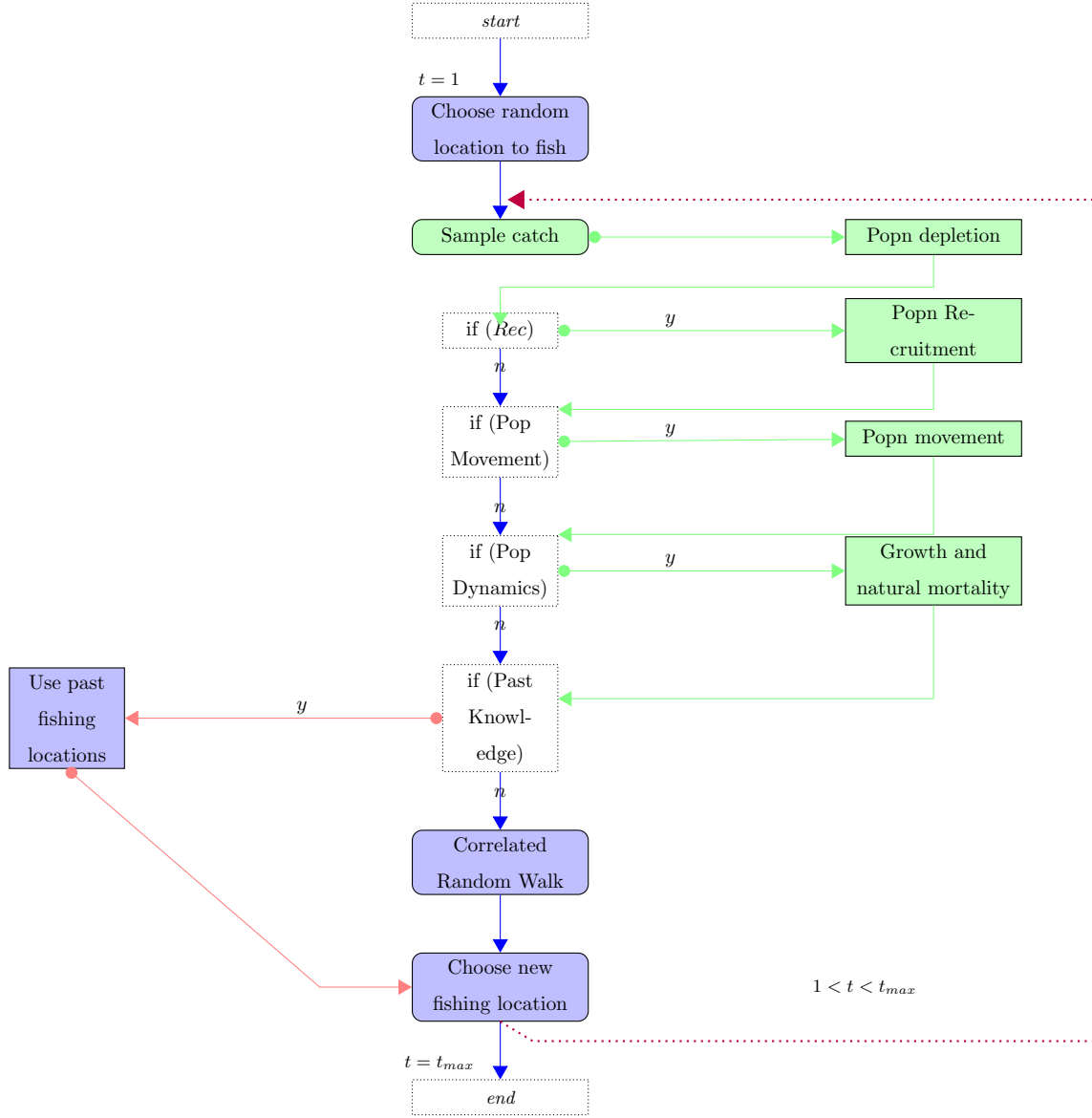


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics)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

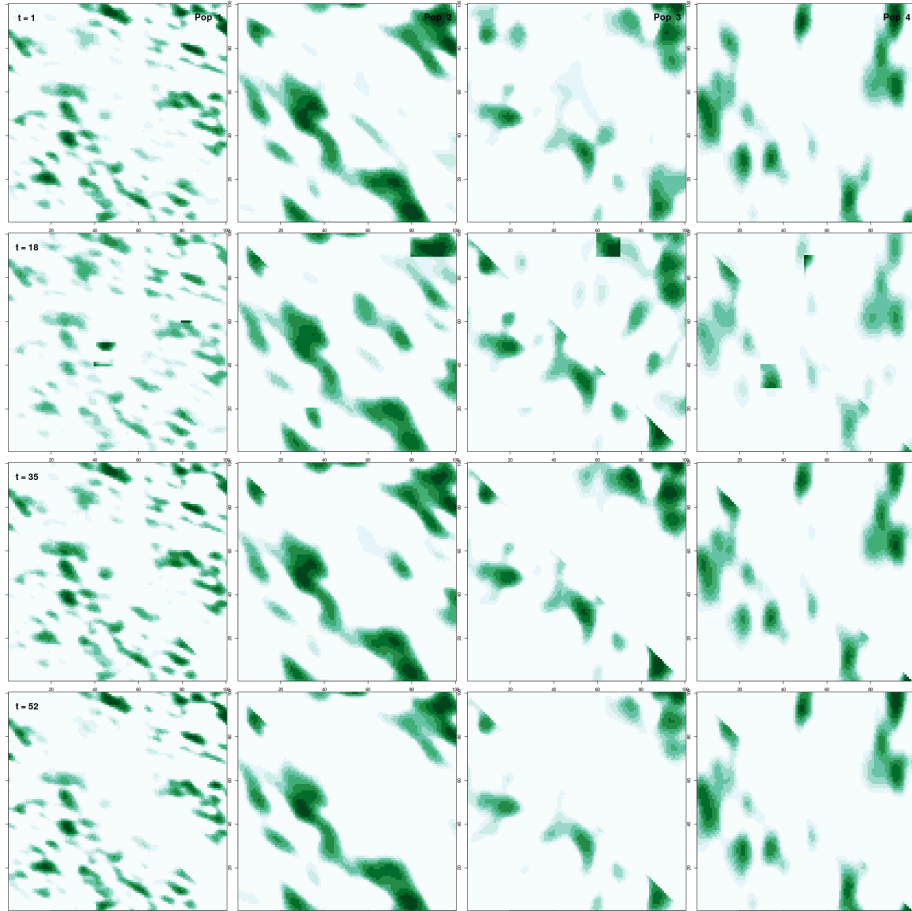


Figure 2: Simulated spatial dynamics - the four populations abundance ($\log+1$) at four time steps.

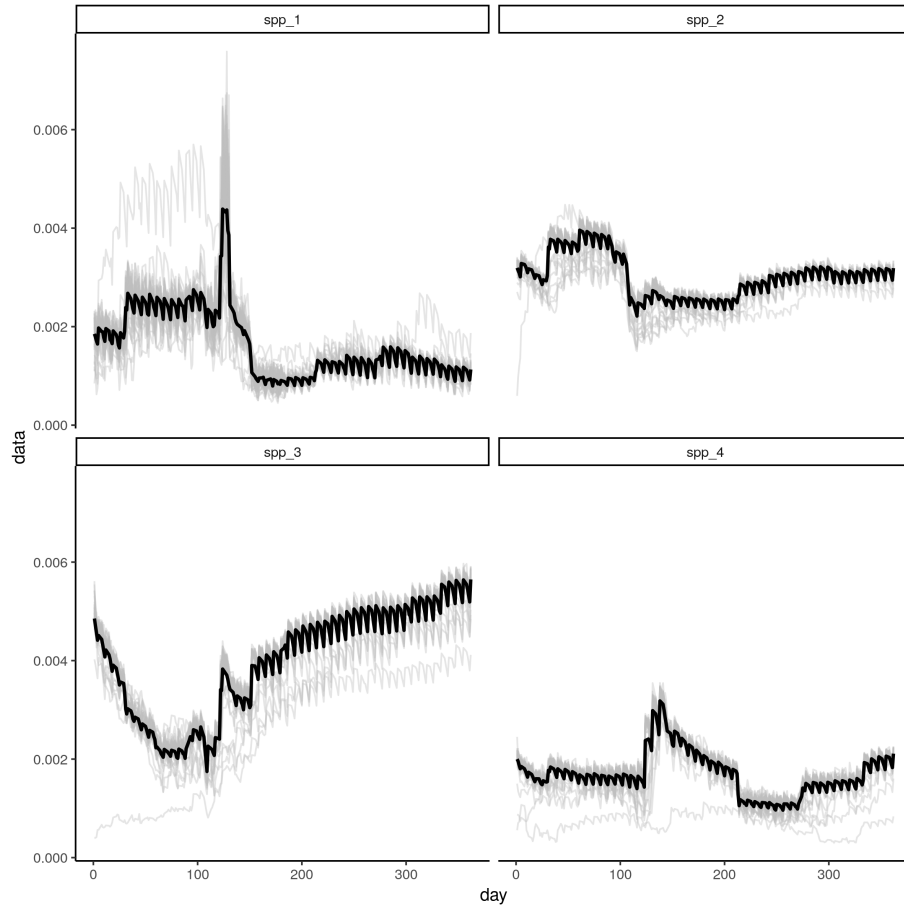


Figure 3: Fishing mortality dynamics - the daily fishing mortalities showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

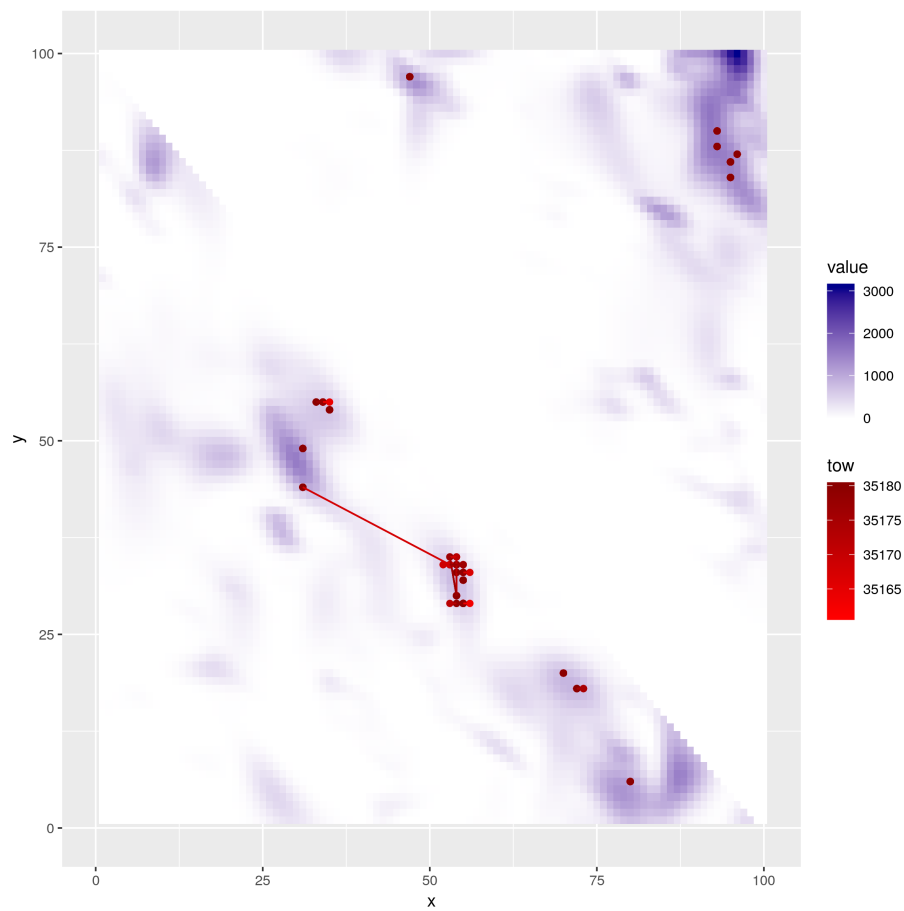


Figure 4: movement of a fleet over a single trip reference overlaid on the value field (i.e. sum of the population abundance \times catchability \times value

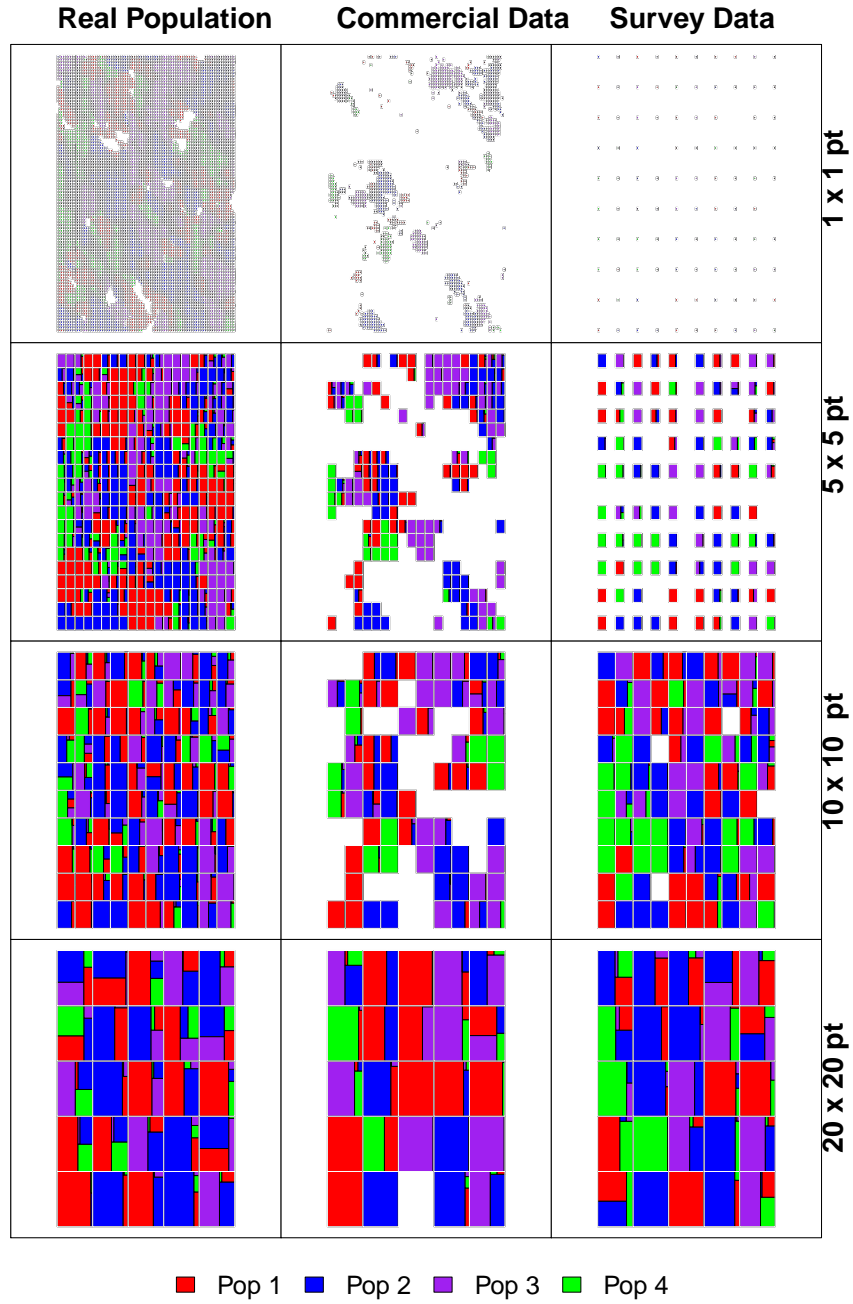


Figure 5: Data aggregation at different spatial resolutions over a ten year period

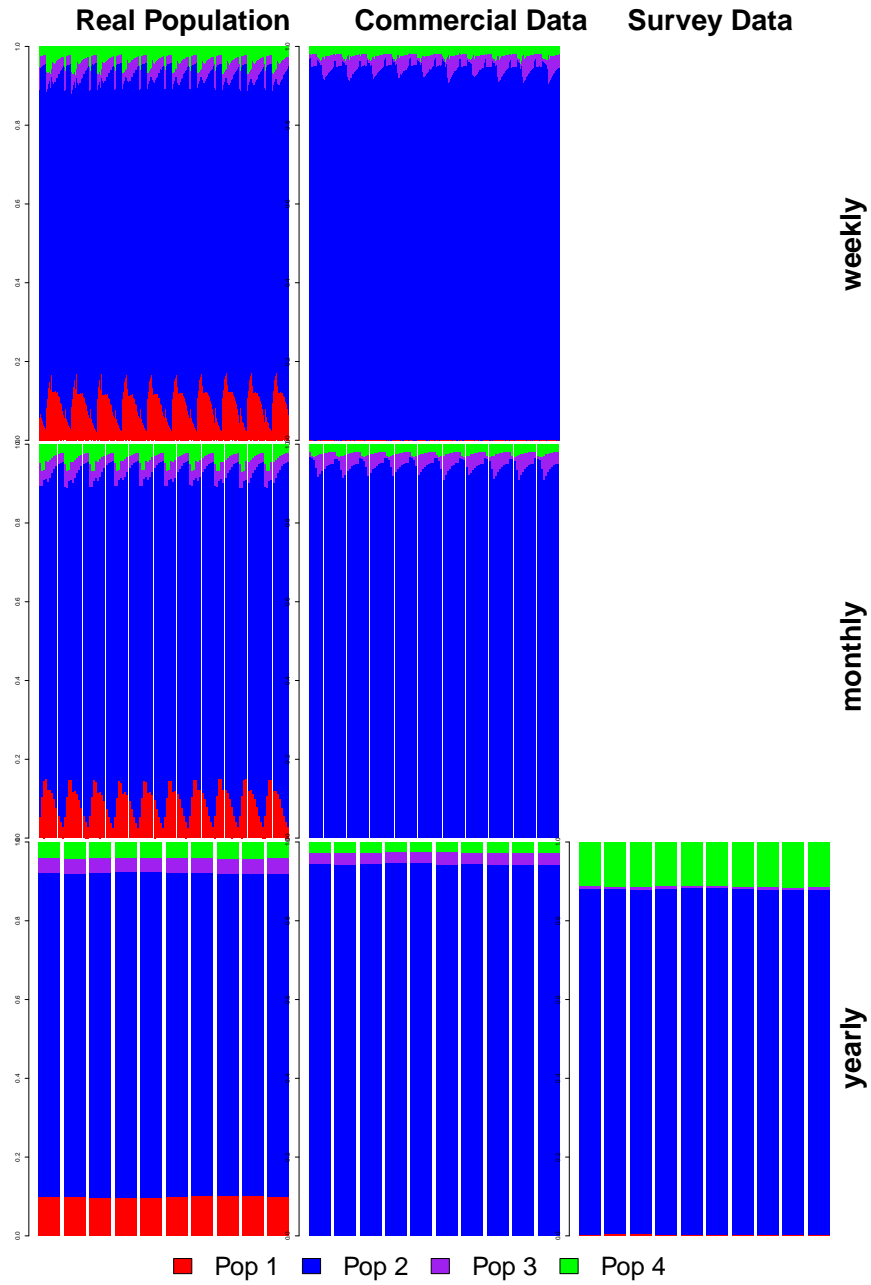


Figure 6: Data aggregation at different temporal resolutions over a ten-year period

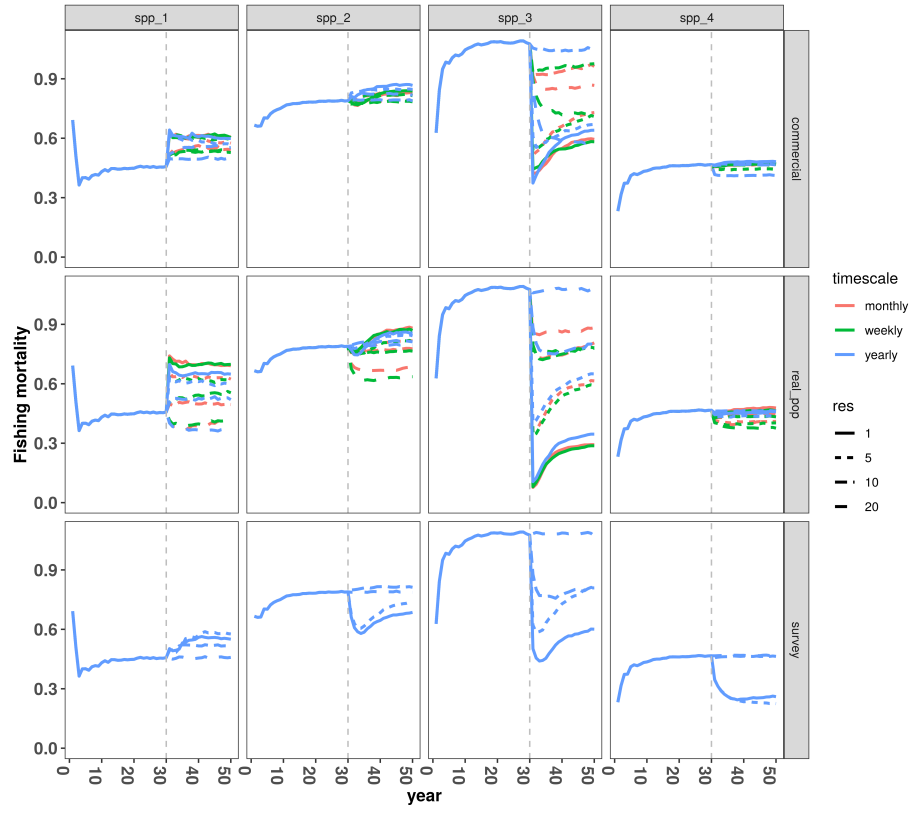


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

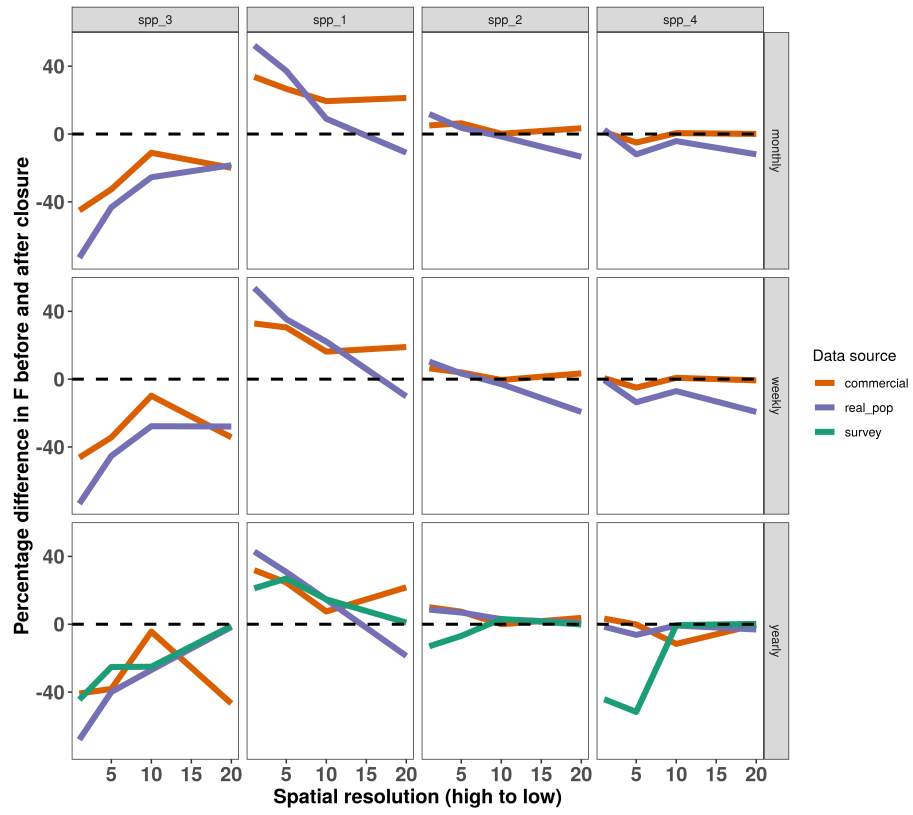


Figure 8: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.



Figure 9: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) species 3 habitat distribution

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