

Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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Abstract

To understand how data resolution impacts inference on mixed fisheries interactions we developed a highly resolved spatiotemporal discrete-event simulation model ('MixFishSim') 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 population targeting under an explore-exploit strategy. This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries. Fifty years of sub-daily fishing activity was simulated and used to draw inference on the underlying community structures. We compared inferences based on: commercial catch, a simulated fixed-site sampling survey design and the true (simulated) underlying populations. 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

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spatial and temporal scale. In application to a mixed fishery exploiting four different populations we found different spatial patterns were evident and that the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. However, aggregation across time periods has less of a negative impact on the closure success and while not as effective as when based on the true population, closures based on high catch rates observed in commercial data could still reduce fishing on a protected species.

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

Keywords: spatiotemporal, mixed fisheries, individual based, spatial management, heterogeneity, preferential sampling

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1. Introduction

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

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

15 adaptive spatial management strategies have been proposed as a way of reduc-
16 ing over-quota discards (Holmes et al., 2011; Little et al., 2015; Dunn et al.,
17 2014). However, if fisheries are to reduce unwanted catch through spatial avoid-
18 ance, an in-depth understanding of spatiotemporal fishery dynamics is required.

19

20 Understanding the correct scale for spatial management measures to be effec-
21 tive is crucial as it enables implementation of effective solutions which minimise
22 economic impact (Dunn et al., 2016). For example, the problem can be to iden-
23 tify a scale that promotes species avoidance for vulnerable or low quota species
24 while allowing continuance of sustainable fisheries for available quota species.
25 Identifying the correct spatial scale remains a challenge because data on fish
26 location at high temporal and spatial resolutions is expensive and difficult to
27 collect and proxies are usually inferred from scientific surveys or commercial
28 catches with limited spatial and temporal resolution. Thus, implementation of
29 spatial measures is hampered by a lack of knowledge of fish and fishery spa-
30 tiotemporal dynamics and understanding of the scale at which these processes
31 become important for management.

32

33

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

44

45 More refined spatiotemporal information has since become available through

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

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

1. Do different source of sampling-derived fisheries data reflect the underlying community structure?
2. How does data aggregation and data source impact on the success of spatial fisheries management measures?

To answer these questions we i) develop a simulation model where population dynamics are highly-resolved in space and time, using a Gaussian spatial process to define suitable habitat for different populations. As the precise locations of the fish are known directly rather than inferred from sampling or commercial catch, we can use the population model to validate how inference from fisheries-dependent and fisheries independent sampling relates to the real community structure in a way we could not with real data. We ii) compare, at different spatial and temporal aggregations, the real (simulated) population distributions to samples from fisheries-dependent and fisheries independent catches

75 to test if these are a true reflection of the relative density of the populations.
76 We then iii) simulate a fishery closure to protect a species based on different
77 spatial and temporal data aggregations.

78

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

81 2. Materials and Methods

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

89

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

95

96 2.1. Population dynamics

97 The basic population level processes were simulated using a modified two-
98 stage Deriso-Schnute delay difference model which models the fish populations in
99 terms of aggregate biomass of recruits and mature components rather than keep-
100 ing track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A
101 daily time-step was chosen to discretise continuous population processes on a bi-
102 ologically relevant and computationally tractable timescale. Population biomass

103 growth was modelled as a function of previous recruited biomass, intrinsic pop-
 104 ulation growth and recruitment functionally linked to the adult population size.
 105 Biomass for each cell c was incremented each day d as follows (the full parameter
 106 list is detailed in Table 1):

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

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

112

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

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

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

124

125 2.2. Recruitment dynamics

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

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

130 where α is the maximum recruitment rate, β the spawning stock biomass (SSB)
 131 required to produce half the maximum stock size, S current stock size and σ^2
 132 the variability in the recruitment due to stochastic processes. The stochastic
 133 Ricker form (Ricker, 1954) is:

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

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

136 2.3. Population movement dynamics

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

144

145 The combined process results in a population structure and movement pat-
 146 tern unique to each population, with population movement occurring on a
 147 weekly basis. The decision to model population movement on a weekly timescale
 148 was to reflect that fish tend to aggregate in species specific locations that have

149 been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).
 150 Therefore this process approximated the demographic shifts in fish populations
 151 throughout a year with seasonal spawning patterns (Figure S1).

152 To simulate fish population distribution in space and time a Gaussian spa-
 153 tial process was employed to model habitat suitability for each of the popula-
 154 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
 155 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
 156 $\{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,
 157 where the correlation strength weakens with distance controlled by two param-
 158 eters, with ν a scale parameter in the units of distance and κ a shape parameter
 159 which determines the smoothness of the process. We use the most commonly
 160 used Matérn covariance structure as it is a flexible form that under certain
 161 conditions is of the same form as an exponential function and itThis enables
 162 us to model the spatial autocorrelation observed in animal populations where
 163 density is more similar in nearby locations, but that correlation decreases non-
 164 linearly (Tobler, 1970; F. Dormann et al., 2007; Poos and Rijnsdorp, 2007b).
 165 We change the parameters to implement different spatial structures for the dif-
 166 ferent populations using the *RandomFields* R package (Schlather et al., 2015).
 167 We define a stationary habitat field with an anisotropic pattern (to simulate a
 168 depth gradient) and combine it with a temporally dynamic thermal tolerance
 169 field to imitate two key drivers of population dynamics without modelling the
 170 processes explicitly. Each population was initialised at a single location, and
 171 subsequently moved across the entire space according to a probabilistic distri-
 172 bution based on habitat suitability (represented by the normalised values from
 173 the GRFs), temperature tolerance and distance from current cell:

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

174 Where $d_{I,J}$ is the euclidean distance between cell I and cell J , λ is a given rate
 175 of decay, $Hab_{c,p}$ is the index of habitat suitability for cell c and population p ,
 176 with $Tol_{c,p,wk}$ the temperature tolerance for cell c by population p in week wk

177 (see below).

178

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

184

185 A time-varying temperature covariate changes the interaction between time
186 and suitable habitat on a weekly time-step. Each population p was assigned a
187 thermal tolerance with mean, μ_p and standard deviation, σ_p so that each cell
188 and population temperature tolerance is defined that:

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

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

193

194 ~~The final combined process results in a population structure and movement~~
195 ~~pattern unique to each population, with population movement occurring on a~~
196 ~~weekly basis. The decision to model population movement on a weekly timescale~~
197 ~~was to reflect that fish tend to aggregate in species specific locations that have~~
198 ~~been observed to last around one to two weeks (Poos et al 2007). Therefore this~~
199 ~~process approximated the demographic shifts in fish populations throughout a~~
200 ~~year with seasonal spawning patterns (Figure S1).~~

201 2.4. Fleet dynamics

202 Fleet dynamics ~~were can be~~ broadly categorised into three components. *Fleet*
203 *targeting* ~~determineddetermines~~ the fleet catch efficiency and preference to-
204 wards a particular population; *trip-level decisions* ~~determinedthat determines~~

the initial location to be fished at the beginning of a trip; and *within-trip decisions* determined fishing locations, that determines movement from one fishing spot to another within a trip. This results in an explore-exploit strategy was implemented in the model that combined these three components for individual vessels to maximise their catch from an unknown resource distribution (Bailey et al., 2019). The decision to use an individual based model for fishing vessels was taken because fishers are heterogeneous in their location choice behaviour due to different objectives, risk preference and targeting preference (Van Putten et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics are emergent from individual dynamics rather than pre-defined group dynamics.

2.4.1. Fleet targeting

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

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

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

234 2.4.3. *Decision about where to fish within a trip*

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

248
 249 For our implementation of a random walk directional change is based on a
 250 negatively correlated circular distribution where a favourable fishing ground is
 251 likely to be “fished back over” by the vessel returning in the direction it came
 252 from. The step length (i.e. the distance travelled from the current to the next
 253 fishing location) is determined by relating recent fishing success, measured as
 254 the summed value of fish caught (revenue, Rev);

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

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

261 relationship:

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

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

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

$$\begin{aligned} \text{when } Br_t < 180, Br_{t+1} &= 180 + \sim vm[(0, 360), k] \\ Br_t > 180, Br_{t+1} &= 180 - \sim vm[(0, 360), k] \end{aligned}$$

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

271 2.4.4. Local population depletion

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

281 2.5. Fisheries independent survey

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

284 survey design). Catches of the populations at each station are recorded but not
285 removed from the population (catches are assumed to have negligible impact
286 on population dynamics). This provides a fishery independent snapshot of the
287 populations at a regular spatial intervals each year, similar to scientific surveys
288 undertaken by fisheries research agencies.

289

290 2.6. Software: R-package development

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

294

295 3. Model calibration

296 We calibrate *MixFishSim* to investigate the influence of data aggregation on
297 spatial inference.

298 3.1. Population models

299 We calibrated the simulation model for four example populations with dif-
300 ferent demographics, growth rates, natural mortality and recruitment (Table 4).
301 Habitat preference (Figure S2) and temperature (Figures S3, with temperature
302 tolerance S4) defined to be unique to each population resulting in differently
303 weekly distribution patterns (Figures S1-S6). In addition, each of the pop-
304 ulations was assumed to have two defined spawning areas that result in the
305 populations moving towards these areas in pre-defined weeks (Figure S7) with
306 population-specific movement rates (Table 4). The population demographics
307 were defined to broadly represent three mobile low-medium value groundfish
308 species and one high value species with low mobility, with the dynamics hypo-
309 thetical but as you might expect to find in a typical demersal fishery.

310 3.2. Fleet calibration

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

321

322 Fishing locations were chosen based on random search and, with increasing
323 proportion as time progressed, experience of profitable catches built up in the
324 same month from previous years and from the previous trip. 'Profitable' in
325 this context was defined as the locations where the top 70 % of expected profit
326 would be found given revenue from previous trips and cost of movement to the
327 new fishing location. This probability was based on a logistic sigmoid function
328 with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate
329 that ensures the upper asymptote (where decisions are mainly based on past
330 knowledge) is reached approximately halfway through the simulation.

331

332 3.3. Survey settings

333 The survey simulation was set up with a fixed gridded station design with
334 100 stations fished each year, starting on day 92 and ending on day 112 (5
335 stations per day) with same catchability parameter ($Q_p = 1$) for all populations
336 p . This approximates a real world survey design with limited seasonal and
337 spatial coverage.

338 *3.4. Example research question*

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

346
347 *How does sampling-derived fisheries data reflect the underlying population*
348 *structure?*

349
350 To answer this question we compare different spatial and temporal aggrega-
351 tions of the true population distributions to:

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

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

361
362 The following steps are undertaken to determine closures:

- 363 1. Extract data source (true population, commercial or survey),
- 364 2. Aggregate according to desired spatial and temporal resolution,

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

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

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

375 We implemented a series of spatial closures targeted at reducing fishing mor-
376 tality on population 3, given the different data sources and spatial and temporal
377 resolutions above. We use the effectiveness of these closures in reducing fishing
378 mortality as a way of evaluating the trade-offs in data sources and resolution.

379 Survey closures were on an annual basis only, as this was the most temporally
380 resolved survey data available. We evaluated the factors contributing to the suc-
381 cess of the closures through a regression tree (using the R package *REEMtree*
382 (Sela and Simonoff, 2011)) to identify the factor most contributing to differences
383 in fishing mortality before and after the closure.

384 4. Results

385 4.1. Emergent simulation dynamics

386 Individual habitat preferences and thermal tolerances result in different spa-
387 tial habitat use for each population (Figure 2) and consequently different sea-
388 sonal exploitation patterns (Figure 3).

It can be seen from a single vessels movements during a trip that the ves-
sel exploits three different fishing grounds, each of them multiple times (Figure

4(A)), while across several trips fishing grounds that are further apart are fished (Figure 4 (B)). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 4 (D), where several vessels tracks are overlaid on the revenue field, i.e.

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

389 Vessels from the same fleet (and therefore targeting preference) may exploit
 390 some shared and some different fishing grounds depending on their own personal
 391 experience during the exploratory phase of the fishery (Figure 4 (C)). This
 392 results from the randomness in the correlated random walk step function, with
 393 distance moved during the exploitation phase and the direction stochastically
 394 related to the revenue experienced on the fishing ground (Figure 4 (D)).

395 4.2. How does sampling-derived fisheries data reflect the underlying population 396 structure?

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

413 emerge.

414

415 Different perceptions of the proportion of each stock in an area are seen when
416 we aggregate the data at different timescales, with weekly (top), monthly (mid-
417 dle) and yearly (bottom) catch compositions from across an aggregated 20 x 20
418 area showing different patterns (Figure 6). In the true population, the monthly
419 aggregation captures the major patterns of composition seen in the weekly data
420 with the percentage of different populations in the catch having similar mean
421 and standard deviations (Table 7). In the weekly and monthly data population
422 2 dominates. However, some of the variation was lost when aggregated to an
423 annual level, as indicated from the lower standard deviations (Table 7).

424

425 The commercial data on a weekly basis shows some of the same patterns as
426 the true population, though the population 1 (in red) is less well represented
427 and some weeks are missing catches from the area. Here, weekly and monthly
428 compositions were nearly identical (Figure 6; Table 7). Again, yearly values
429 head a similar mean but smaller standard deviation.

430

431 The survey data was only available on an annual basis, and showed again
432 a slightly different composition from the true population and the commercial
433 data; in particular a greater proportion of population 4 (Figure 6).

434 4.3. How does data aggregation and source impact on spatial fisheries manage- 435 ment measures?

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

441 In most cases the fishery closure was successful in reducing fishing mortal-
442 ity on the species of interest (population 3; Figure 7), though interestingly the

largest reductions in fishing mortality happened immediately after the closures, following which the fisheries “adapted” to the closures by finding new areas of high abundance to fish 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 (i.e. failed to reduce fishing mortality) 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.

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. We found that these trade-offs existed, with high catches maintained with an effective closure when the highest resolution data was used, with the effect being linear when the true population distribution was known and also persisting for closures based on commercial information (Figure 10).

472 5. Discussion

473 Our study presents a new highly resolved fisheries simulation framework to
474 evaluate the importance of data scaling and considers potential bias introduced
475 through data aggregation when using fisheries data to infer spatiotemporal dy-
476 namics of fish populations. Understanding how fishers exploit multiple hetero-
477 geneously distributed fish populations with different catch limits or conservation
478 status requires detailed understanding of the overlap of resources; this is difficult
479 to achieve using conventional modelling approaches due to species targeting in
480 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
481 ten data are aggregated or extrapolated which requires assumptions about the
482 spatial and temporal scale of processes. Our study explores the assumptions
483 behind such aggregation and preferential sampling to identify potential impacts
484 on management advice. With modern management approaches increasingly
485 employing more nuanced spatiotemporal approaches to maximise productivity
486 while taking account of both the biological and human processes operating on
487 different time-frames (Dunn et al., 2016), understanding assumptions behind
488 the data used - increasingly a combination of logbook and positional informa-
489 tion from vessel monitoring systems - is vital to ensure measures are effective.

491 5.1. Simulation dynamics

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

497
498 Our approach is unique in that it captures fine scale population and fish-
499 ery dynamics and their interaction in a way not usually possible with real data
500 and thus not usually considered in fisheries simulations. While other simulation

501 frameworks seek to model individual vessel dynamics based on inferred dynam-
502 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
503 identify measures to meet particular management goals (Bailey et al., 2019), our
504 framework allows users to explore the assumptions in modelling observational
505 data and evaluate the underlying dynamics of such approaches at a fine spatial
506 and temporal scale. This offers the advantage that larger scale fishery patterns
507 are emergent properties of the system and results can be compared to those
508 obtained under a statistical modelling framework.

509

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

521

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

529

530 We take account of heterogeneity in fleet dynamics due to different prefer-
531 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an

individual vessel rather than fleet level. We do not explicitly define fleets as rational profit maximisers at the outset, but consider there are several stages to development of the fishery; information gathering through search where the resource location is not known, followed by individual learnt behaviour of profitable locations. This provides a realistic model of how fishing patterns are established and maintained to exploit an uncertain resource through an explore-exploit strategy (Mangel and Clark, 1983; Bailey et al., 2019).

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

Our results demonstrate the importance of considering data scale and resolution when using observational data to support management measures. We find that understanding of the community composition dynamics will depend on the level of data aggregation and its important to consider the scale of processes; including population movement rates, habitat uniformity and fishing targeting practices if potential biases in data are to be understood and taken into account (Figures 2, 4).

Our simulation shows that, despite biases introduced through the fishing process, the commercially derived data could still inform on the key spatial patterns in the community structures where the fisheries occurred, which was spatially limited due to the “hotspots” of commercially valuable species being fished. Similarly, despite the even spatial coverage the survey was able to capture some of the same spatial patterns as the true population, but missed others due to gaps between survey stations limiting spatial and temporal coverage (Figure 5). This provides a challenge when modelling unsampled areas in inferring species distribution maps, though these limitations may be overcome by understanding the relationship between the species and habitat covariates where these are known at unsampled locations (Robinson et al., 2011).

561 *5.3. How does data aggregation and source impact on spatial fisheries manage-*
562 *ment measures?*

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

567
568 The yearly data assumes the same proportion of each population caught at
569 any time of the year due to the data aggregation. This assumption introduces
570 ‘aggregation bias’ as the data may only be representative of some point (or no
571 point) in time. The monthly data shows some consistency between the real pop-
572 ulation and commercial data for population 2 - 4, though population 1 remains
573 under-represented. On an annual basis, interestingly the commercial data un-
574 der represents the first species (in red) while the survey over represents species
575 1. This is likely due to the biases in commercial sampling, with the fisheries
576 not targeting the areas where population 1 are present and the survey sampling
577 areas where population 1 is more abundant than on average. This indicates that
578 fixed closures, at the right resolution, when based on commercially derived data
579 have the potential to reduced fishing mortality. The likely cost of poor spatial
580 and temporal resolution is associated with reduced effectiveness and potentially
581 closing fishing opportunities for other fisheries (Figure 10).

582
583 Two contrasting real world approaches in this respect were the spatial clo-
584 sures to protect cod in the North Sea. In one example, large scale spatial closures
585 were implemented with little success due to effort displacement to previously
586 unfished areas (Dinmore et al., 2003), while in another small scale targeted
587 spatiotemporal closures were considered to have some effect in reducing cod
588 mortality without having to disrupt other fisheries substantially (Needle and
589 Catarino, 2011). These examples emphasise the importance of considering the
590 right scale and aggregation of data when identifying area closures and the need
591 to consider changing dynamics in the fisheries in response to such closures.

592

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

598 *5.4. Model assumptions and caveats*

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

603

604 Fish populations in our simulations move in pre-defined timescales and ac-
605 cording to fixed habitat preferences and temperature gradients (Figures S2, S3).
606 Our assumptions in calibrating the model (movement rates, temperature toler-
607 ances) will have a direct impact on our conclusions on the relative importance
608 of spatial and temporal processes. These assumptions could be explored in a
609 future study by varying the parameters and assessing the robustness of our con-
610 clusions. For our example application we have chosen movement rates to reflect
611 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

612

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

621

622 5.5. Future applications of *MixFishSim*

623 We consider that the increased availability of high resolution catch and lo-
624 cational information from commercial fisheries will require it to be a key source
625 of data for ensuring management is implemented at the right scale in future.
626 For example, identifying hot-spots for bycatch reduction or identifying spatial
627 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little
628 et al., 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has
629 the potential to test some of the assumptions behind the modelling approaches
630 in identifying such hotspots and indeed behind spatiotemporal modelling in
631 general, (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical
632 models under different data generation processes as exemplified by Stock et al.
633 (2019)deleted).

634
635 Other novel applications of our framework could be: testing different sur-
636 vey designs given multiple species and data generating assumptions (Xu et al.,
637 2015); commercial index standardisation methods and approaches and under-
638 standing of appropriate scales and data aggregations and non-proportionality
639 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
640 exploring assumptions about the distribution of natural mortality and fishing
641 mortality throughout the year and importance of capturing in-year dynamics
642 in estimating stock status (Liu and Heino, 2014); at sea sampling scheme de-
643 signs to deliver unbiased estimates of population parameters (Cotter and Pilling,
644 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn
645 et al., 2016); testing the ability of commonly employed fleet dynamics models
646 such as Random Utility Models to capture fine scale dynamics and understand
647 their importance (Girardin et al., 2017); and as a detailed operating model in a
648 management strategy evaluation (Mahévas and Pelletier, 2004).

649

650 6. Conclusions

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

659
660 Our application shows that inference on community dynamics may change
661 depending on the scale of data aggregation. There is an important balance in
662 ensuring that the data are sufficiently spatially and temporally disaggregated
663 that the main features of the data are captured, yet maintaining enough data
664 coverage that the features can be distinguished. We found in our application
665 that there was greater spatial heterogeneity than temporal heterogeneity and
666 that when using aggregated data to define spatial closures coarser temporal reso-
667 lution (months instead of weeks) could still achieve the same results in reducing
668 exploitation rates of a vulnerable species at the highest temporal resolution
669 data. Conversely, reducing the spatial resolution had a negative effect on the
670 effectiveness of the measures (though importantly, there was still some benefit
671 even with coarse spatial resolution).

672
673 While any findings are likely to be case specific, our findings emphasise the
674 need to understand population demographics, habitat use and movement rates
675 in designing any closure scenario based on observational sampling. This infor-
676 mation can then be used to set the bounds on data aggregation used in modelling
677 studies aimed at informing the management measures.

678
679 *MixFishSim* has numerous potential additional applications as it enables

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

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691 **Appendices**

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

Variable	Meaning	Units
Population dynamics		
<i>Delay-difference model</i>		
$B_{c,d}$	Biomass in cell c and day d	kg
$Z_{c,d}$	Total mortality in cell c for day d	-
$R_{c,\bar{y}}$	Annually recruited fish in cell	yr ⁻¹
ρ	Brody's growth coefficient	yr ⁻¹
Wt_R	Weight of a fully recruited fish	kg
Wt_{R-1}	Weight of a pre-recruit fish	kg
α_d	Proportion of annually recruited fish recruited during day d	-
<i>Baranov catch equation</i>		
$C_{c,d}$	Catch from cell c for day d	kg
$F_{c,d}$	Instantaneous rate of fishing mortality in cell c on day d	-
$M_{c,d}$	Instantaneous rate of natural mortality in cell c on day d	-
$B_{c,d}$	Biomass in cell c on day d	kg
Recruitment dynamics		
$\tilde{R}_{c,d}$	is the recruitment in cell c for day d	d^{-1}
$B_{c,d}$	biomass in cell c for day d	d^{-1}
α	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	kg
β	the stock size required to produce half the maximum rate of recruitment (Beverton Holt) or density dependent reduction in productivity per capita of SSB	kg

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

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

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

Variable	Meaning	Units
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg^{-1}
Le	Step length for vessel	-
Br	Bearing	degrees
k	Concentration parameter for von mises distribution	-
β_1	shape parameter for step function	-
β_2	shape parameter for step function	-
β_3	shape parameter for step function	-

Table 4: Population dynamics and movement parameter settings.

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn ν	1/0.015	1/0.05	1/0.01	1/0.005
Matérn κ	1	2	1	1
Anisotropy	1.5,3,-3,4	1,2,-1,2	2.5,1,-1,2	0.1,2,-1,0.2
Spawning areas (bound box)	40,50,40,50; 80,90,60,70	50,60,30,40; 80,90,90,90	30,34,10,20; 60,70,20,30	50,55,80,85; 30,40,30,40
Spawning multiplier = 10				
Movement $\lambda = 0.1$				
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit α	6	27	18	0.3
Beverton-Holt Recruit β	4	4	11	0.5
Beverton-Holt Recruit σ^2	0.7	0.6	0.7	0.6
Recruit week	13-16	12-16	14-16	16-20
Spawn week	16-18	16-19	16-18	18-20
$K = 0.3$				
$wt = 1$				
$wt_{d-1} = 0.1$				
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ_p	12	15	17	14
σ_p^2	8	9	7	10

Table 5: Fleet dynamics parameter setting.

Parameter	Fleet 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences	pop 2/4	pop 1/3	-	pop 4	pop 2/3
Price $Pr_p1 = 100$					
Price $Pr_p2 = 200$					
Price $Pr_p3 = 350$					
Price $Pr_p4 = 600$					
Q_p	0.01	0.02	0.02	0.01	0.01
Q_p	0.02	0.01	0.02	0.01	0.03
Q_p	0.01	0.02	0.02	0.01	0.02
Q_p	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_3 , the land- ings value n th quantile	90	90	85	90	80
step function $rate$	20	30	25	35	20
Past Knowledge = TRUE					
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios on population 3 (ordered by most effective first). The fishing mortality rate before the closure was 1.08.

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

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

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

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

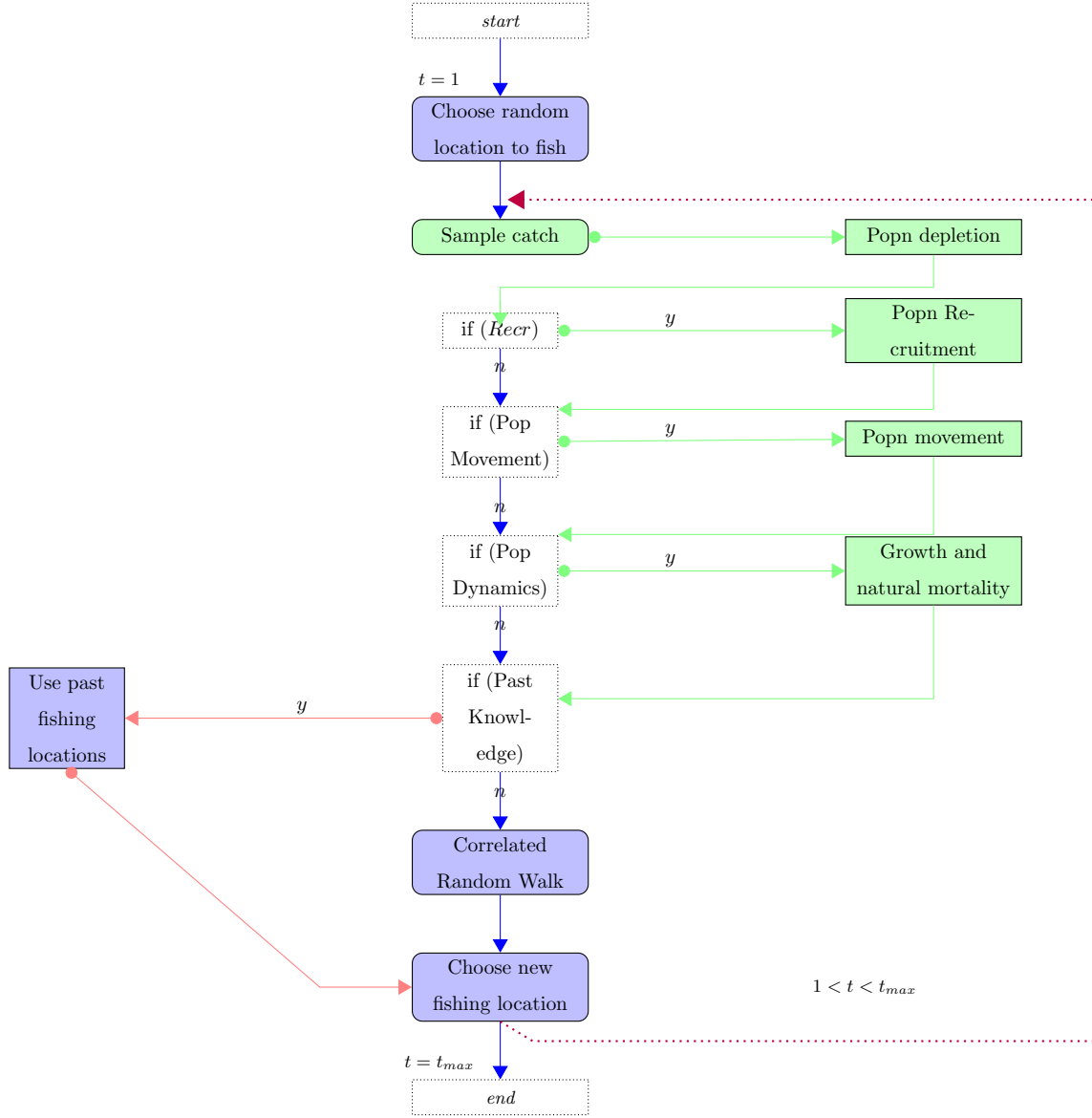


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (*Recr*), (*Pop Movement*), (*Pop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

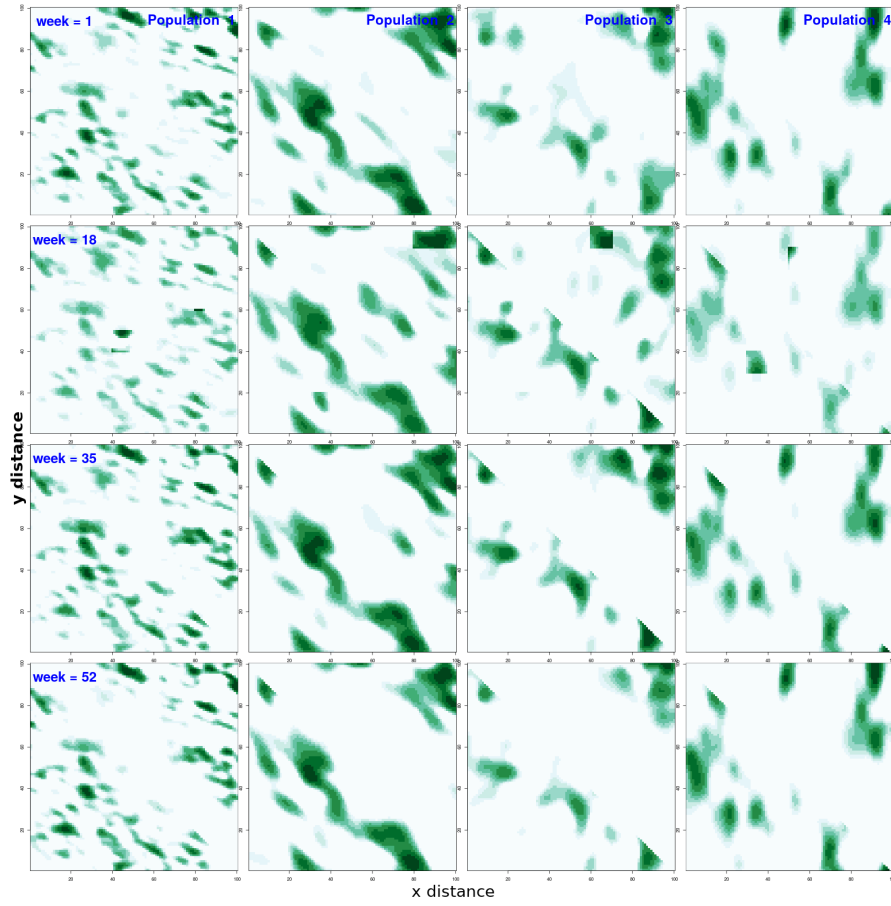


Figure 2: Spatial density (log abundance) for each of the four populations at four time steps. The darker the colour the greater the density of the population. Note that a diagonal anisotropic pattern (mimicking a depth gradient) can be clearly seen in populations 2 and 3. The concentrated spawning areas are also visible in the second row of the panels ($t=18$).

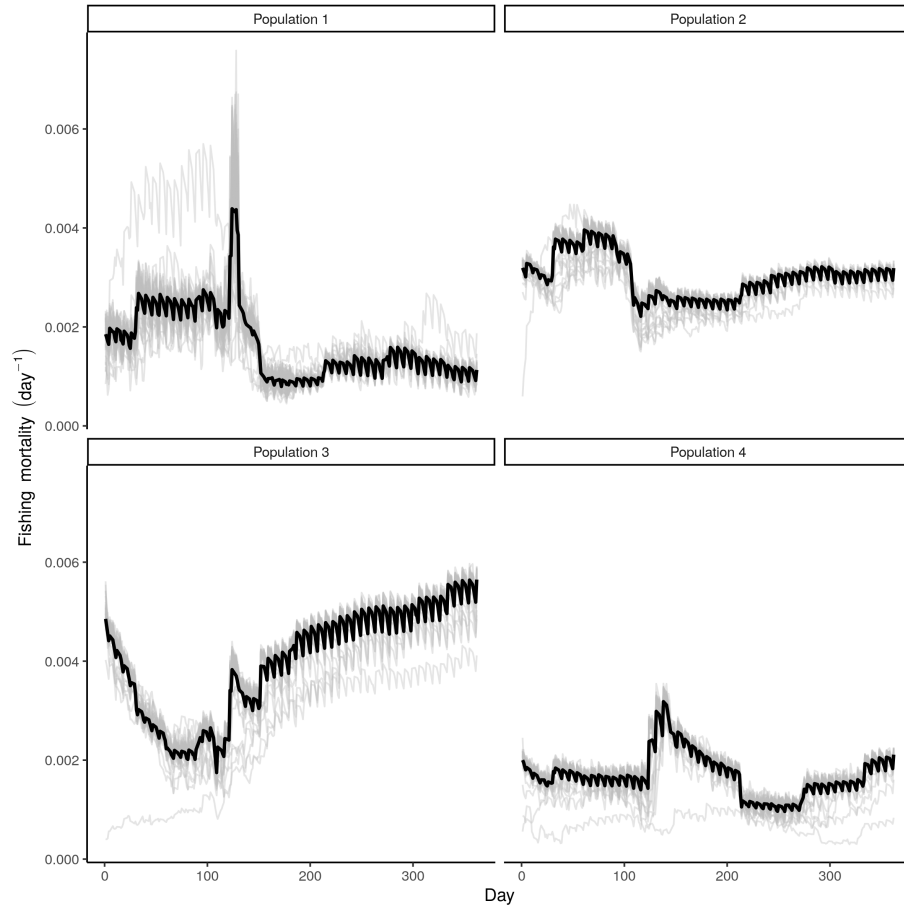


Figure 3: Fishing mortality dynamics - the daily fishing mortalities across the entire spatial domain showing weekly and seasonal patterns in exploitation. Individual years are the light grey lines, the mean of all years the thick black line.

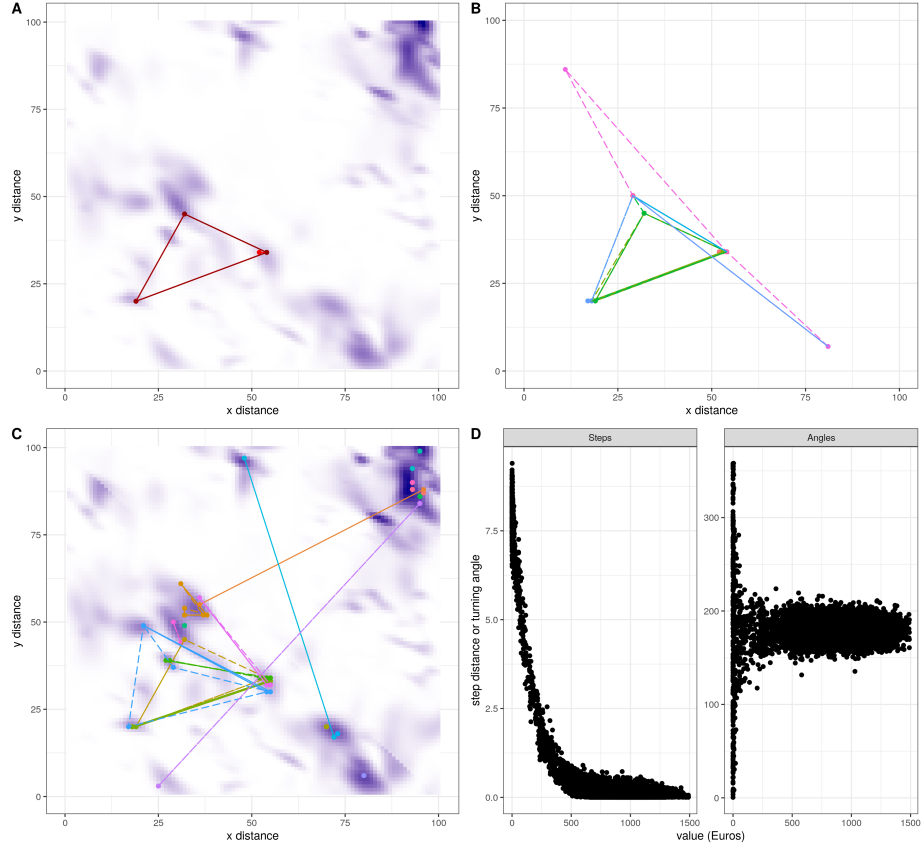


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are a mixture of correlated random walk (solid lines) and experience-based (dashed lines), and that the field is wrapped on a torus so that opposite sides of the spatial domain are considered spatially close; (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation.

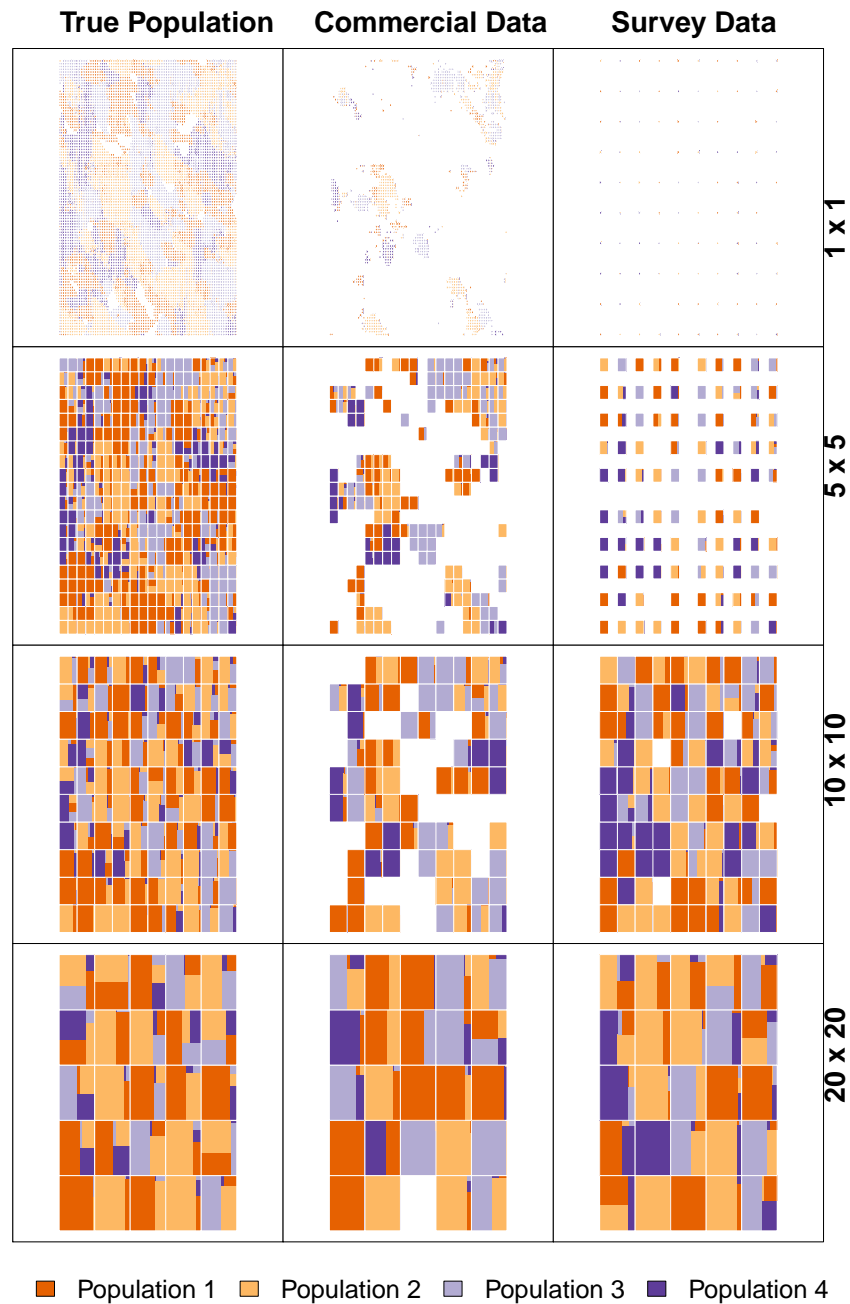


Figure 5: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportionate to the weight of each population caught in that unit. Figure produced using the R package 'mapplots' (Gerritsen (2014)).

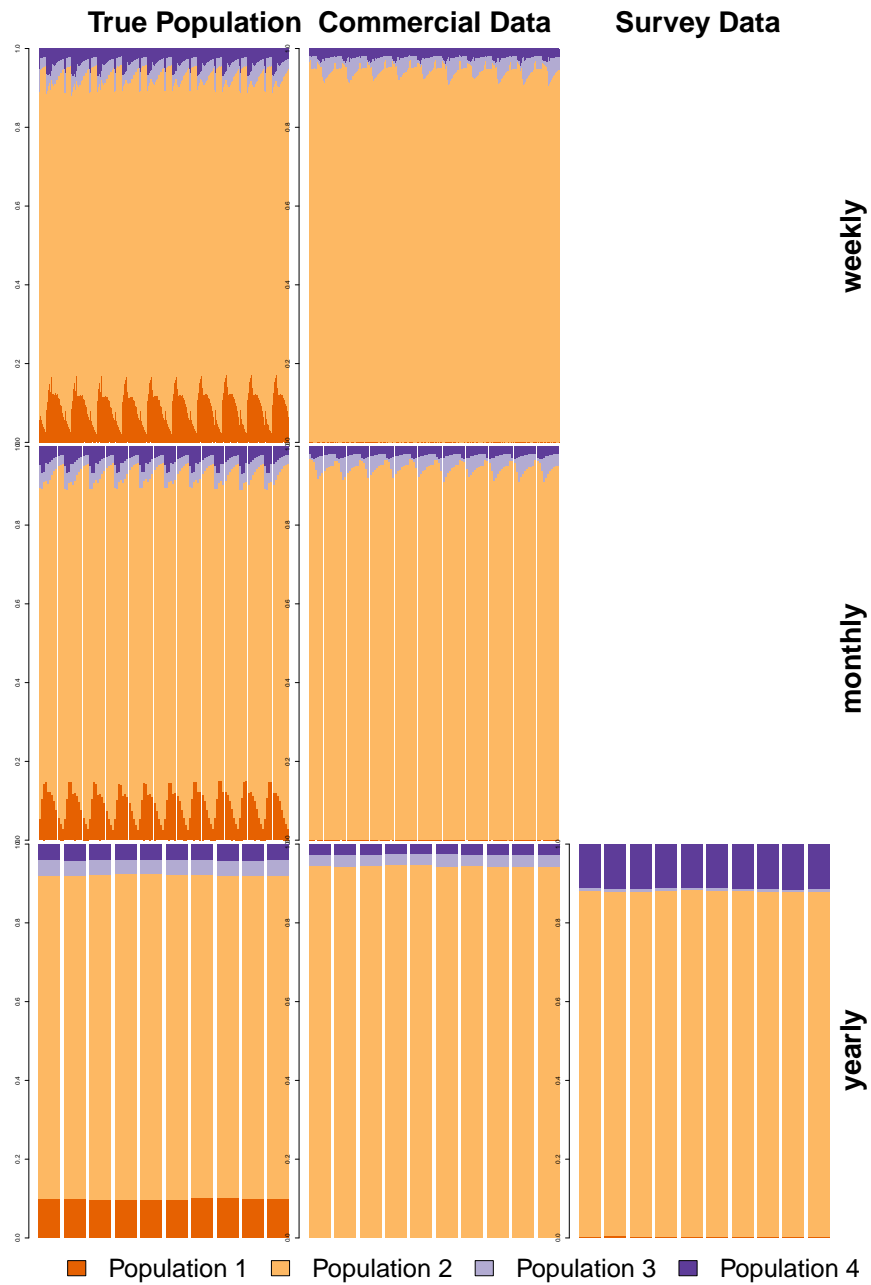


Figure 6: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

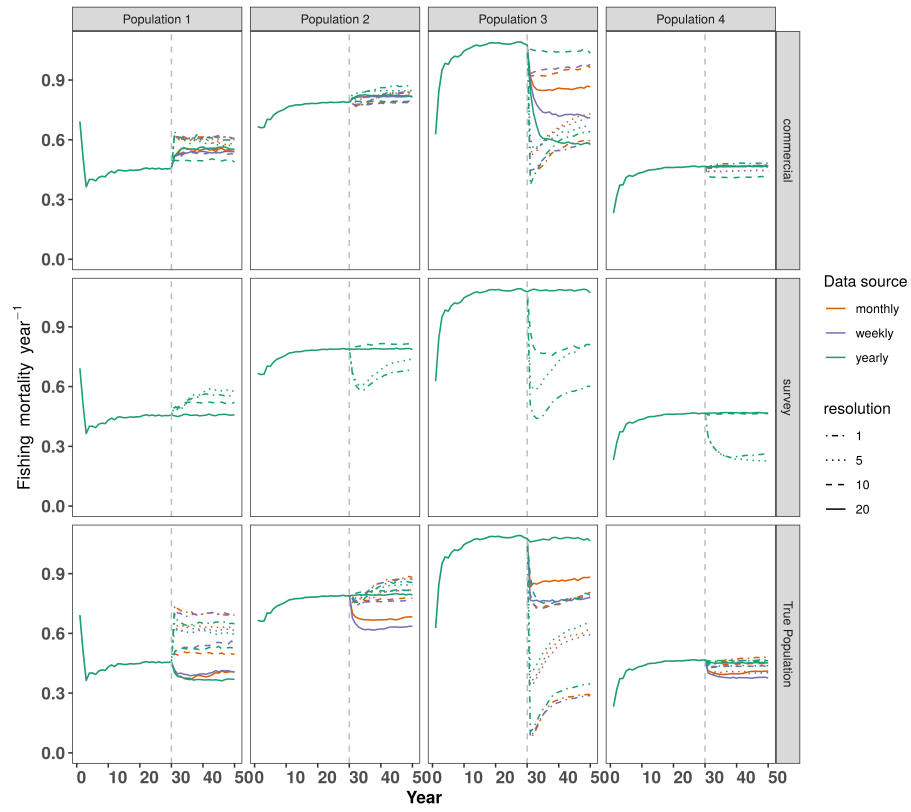


Figure 7: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

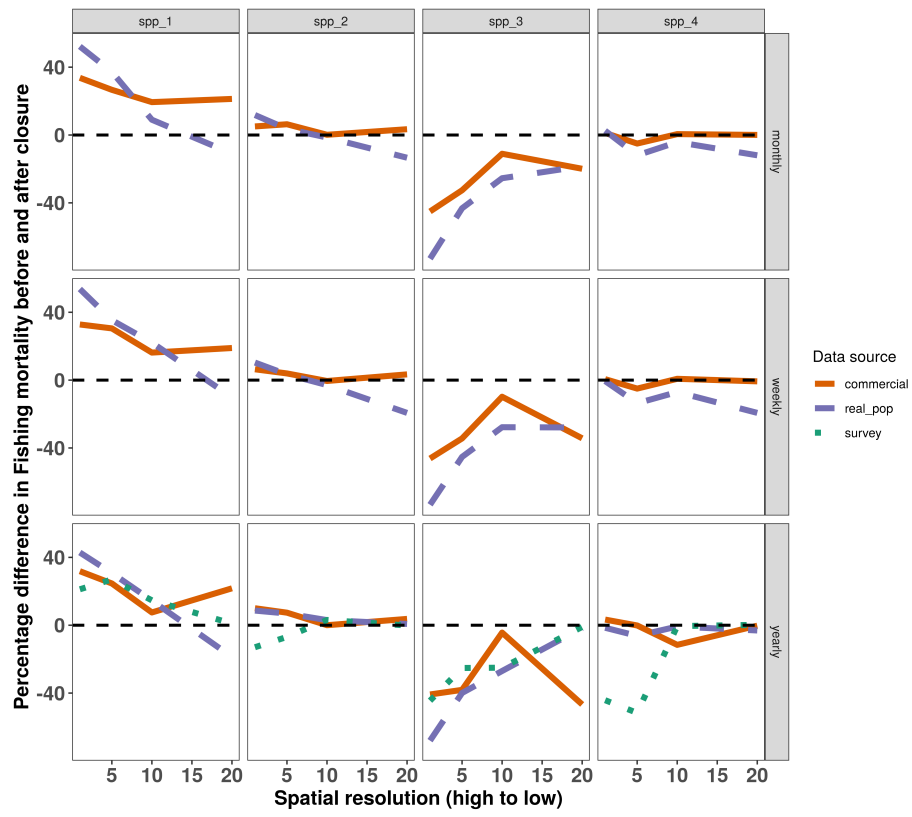


Figure 8: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

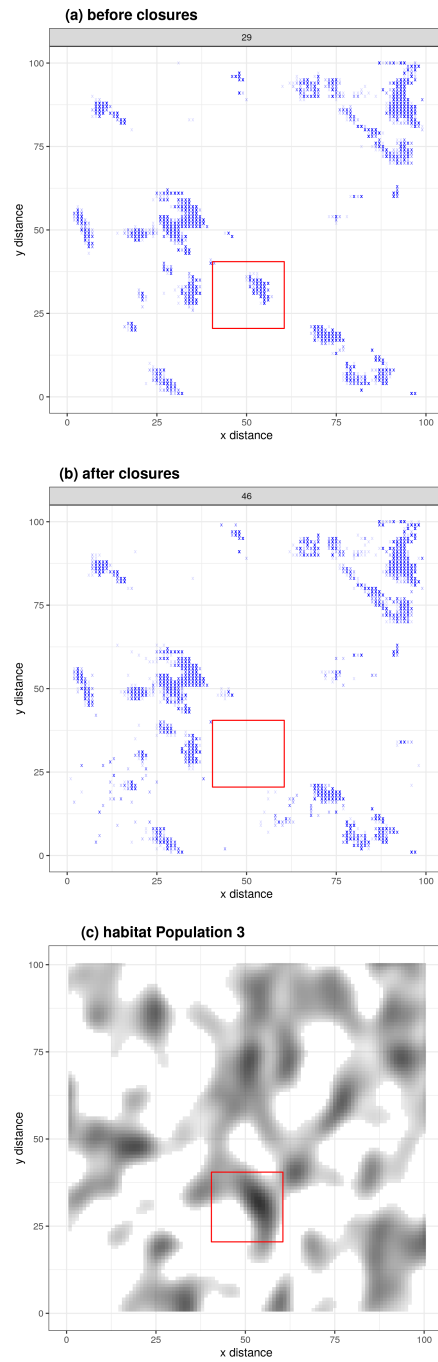


Figure 9: The location of fishing effort before the spatial closure (a) and after the spatial closure (b), and the suitable habitat for population 3 (c). The site of the closure can be seen in the red box on all three panels.

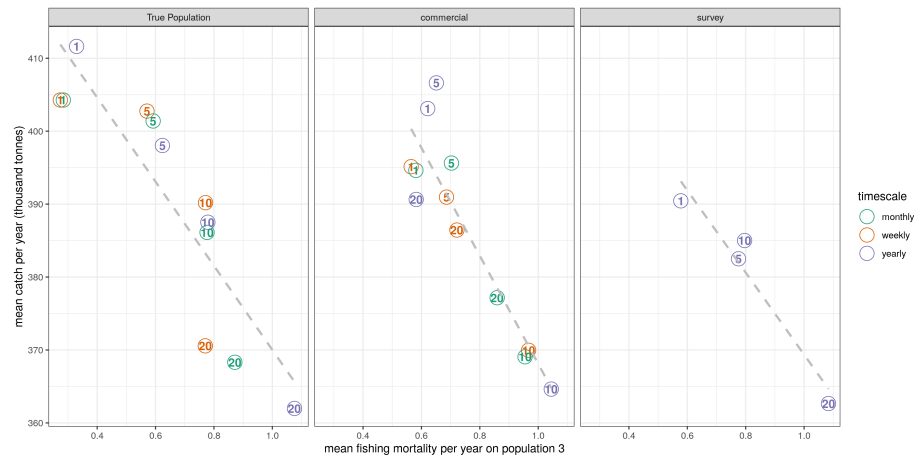


Figure 10: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the direction of the trade-off between reducing fishing mortality and overall catches.

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