

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 discrete-event 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 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 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

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spatial and temporal scale. 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. [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. If fishers discard over-quota catch of a species for which they have no quota, 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; 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.

18

Understanding the correct scale for spatial management measures to be effective is crucial as it enables implementation of effective solutions which minimise economic impact (Dunn et al., 2016). For example, the problem can be to iden-

tify a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species. Identifying the correct spatial scale remains a challenge because data on fish location at high temporal and spatial resolutions is expensive and difficult to collect and proxies are usually inferred from scientific surveys or commercial catches with limited spatial and temporal resolution. Thus, implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which these processes become important for management.

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

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., 2016) 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., 2018) 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

53 areas of high abundance. There is a need to understand the influence of these
54 biases on any spatial management measures which are implemented based on
55 inference from commercial landings or catch data.

56

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

- 61 1. Do different source of sampling-derived fisheries data reflects the underly-
62 ing community structure?
- 63 2. How does data aggregation and data source impact on the success of spa-
64 tial fisheries management measures?

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

77

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

80 2. Materials and Methods

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

88
 89 Population dynamics operate on a daily time-step, while population move-
 90 ment occurs on a weekly time-step, with the fishing module operating on a
 91 tow-by-tow basis (i.e. multiple events a day).

92 2.1. Population dynamics

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

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

103 where ρ is Brody's coefficient, shown to be equal to e^{-K} when K is the growth
 104 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 re-
cruited weight. α_d represents the proportion of fish recruited during that day
for the year, while $R_{c,\tilde{y},d}$ is the annual recruits in year y and day d for cell c .

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 $F_{c,d}$:

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

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 is the sum of those across all fleets
and vessels, $C_{c,d} = \sum_{fl=1}^{fl} \sum_{v=1}^v E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$ with fl and v the fleet and vessel
respectively and $E_{fl,v,c,d}$ and Q_{fl} fishing effort and catchability of the gear, and
 $D_{c,d}$ is the density of the population at the location fished.

2.2. Recruitment dynamics

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

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

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \sigma^2)]$$

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, the stochastic

128 Ricker form (Ricker, 1954):

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

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

131 2.3. Population movement dynamics

132 Population movement is a combination of directed (advective) movement
133 where at certain times of year the population moves towards spawning grounds
134 by increasing the probabilities of moving into the spawning grounds from adja-
135 cent cells, and random (diffusive) movement, governed by a stochastic process
136 where movement between adjacent cells is described by a set of probabilities.

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

the GRFs), temperature and distance from current cell:

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

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

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

A time-varying temperature covariate changes the interaction between time and suitable habitat on a weekly time-step. Each population p was assigned a thermal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population temperature suitability is defined that:

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

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

The final combined process results in a population structure and movement pattern unique to each population, with population movement occurring on a weekly basis. The decision to model population movement on a weekly timescale was to reflect that fish tend to aggregate in species specific locations that have been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts in fish populations

179 throughout a year with seasonal spawning patterns (Figure S5).

180 2.4. Fleet dynamics

181 Fleet dynamics can be broadly categorised into three components: fleet tar-
182 geting - that determined the fleet catch efficiency and preference towards a
183 particular population; trip-level decisions, that determines the initial location
184 to be fished at the beginning of a trip; and within-trip decisions, that determines
185 movement from one fishing spot to another within a trip. An explore-exploit
186 type strategy was implemented in the model that combined these three compo-
187 nents for individual vessels to maximise their catch from an unknown resource
188 distribution (Bailey et al., 2018). The decision to use an individual based model
189 for fishing vessels was taken because fishers are heterogeneous in their location
190 choice behaviour due to different objectives, risk preference and targeting prefer-
191 ence (Van Putten et al., 2012; Boonstra and Hentati-Sundberg, 2015). Therefore
192 fleet dynamics are emergent from individual dynamics rather than pre-defined
193 group dynamics.

194 2.4.1. Fleet targeting

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

202 2.4.2. Decision about where to fish at the start of the trip

203 Several studies (Girardin et al., 2016, for a review) have confirmed past
204 activity and past catch rates are strong predictors of fishing location choice.
205 For this reason, the fleet dynamics sub-model included a learning component,
206 where a vessel's initial fishing location in a trip was based on selecting from
207 previously successful fishing locations. This was achieved by calculating an

208 expected revenue based on the catches from locations fished in the preceding
 209 trip as well as the same month periods in previous years and the travel costs
 210 from the port to the fishing grounds. Then a vessel chooses randomly from the
 211 top 75 % of fishing events as defined by the expected profit, that has a seasonal
 212 component.

213 *2.4.3. Decision about where to fish within the trip*

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

227

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

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

234 where $L_{c,d,p}$ is landings of a population p , and Pr_p price of a population. All
 235 population prices were kept the same across fleets and seasons. Here, when

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

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

241 Where β_1 , β_2 and β_3 are parameters determining the shape of the step function
 242 in its relation to revenue, so that, a step from (x1,y1) to (x2, y2) is defined by:

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

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

243 where Le is the step length, k the concentration parameter from the von Mises
 244 distribution that we correlate with the revenue so that $k = (Rev + 1/RefRev) \cdot$
 245 max_k , where max_k is the maximum concentration value, k , and $RefRev$ is
 246 parametrised as for β_3 in the step length function.

247 2.4.4. Local population depletion

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

257 2.5. Fisheries independent survey

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

265

266 2.6. Software: R-package development

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

270

271 3. Parameterisation

272 We parameterise *MixFishSim* to investigate the influence of data aggregation
273 on spatial inference.

274 3.1. Population models

275 We parametrised the simulation model for four example populations with
276 different demographics, growth rates, natural mortality and recruitment pa-
277 rameters (Table 4). Habitat preference (Figure S1) and temperature tolerances
278 (Figures S3, S4) were defined to be unique to each population resulting in dif-
279 ferently weekly distribution patterns (Figures S5-S7). In addition, each of the
280 populations was assumed to have two defined spawning areas that result in the
281 populations moving towards these areas in pre-defined weeks (Figure S2) with
282 population-specific movement rates (Table 4).

283 3.2. Fleet parametrisation

284 The fleets were parametrised to reflect five different characteristic fisheries
285 with unique exploitation dynamics (Table 5). By setting different catchability
286 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
287 and hence spatial dynamics. The learned random walk process implies that
288 within a fleet different vessels have different spatial distributions based on indi-
289 vidual experience. The step function was parametrised dynamically within the
290 simulations as the maximum revenue obtainable was not known beforehand.
291 This was implemented so that vessels take smaller steps when fishing at a loca-
292 tion that yields landings value in the top 90th percentile of the value experienced
293 in that year so far (as defined per fleet in Table 5).

294
295 Fishing locations were chosen based on random search and, with increasing
296 proportion as time progressed, experience of profitable catches built up in the
297 same month from previous years and from the previous trip. 'Profitable' in
298 this context was defined as the locations where the top 70 % of expected profit
299 would be found given revenue from previous trips and cost of movement to the
300 new fishing location. This probability was based on a logistic sigmoid function
301 with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate
302 that ensures the upper asymptote (where decisions are mainly based on past
303 knowledge) is reached approximately halfway through the simulation.

304

305 3.3. Survey settings

306 The survey simulation was set up with a fixed gridded station design with
307 100 stations fished each year, starting on day 92 and ending on day 112 (5
308 stations per day) with same catchability parameters for all populations ($Q_p =$
309 1). This approximates a real world survey design with limited seasonal and
310 spatial coverage.

311 *3.4. Example research question*

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

319

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

322

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

- 325 a) **fisheries-independent data:** the inferred population density from a
326 fixed-site sampling survey design as commonly used for fisheries monitor-
327 ing purposes;
- 328 b) **fisheries-dependent data:** the inferred population density from our
329 fleet model that includes fishery-induced sampling dynamics.

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

334

335 The following steps are undertaken to determine closures:

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

338 3. Interpolate across entire area at desired resolution using simple bivariate
 339 interpolation using the *interp* function from the R package akima (Akima,
 340 2006). This is intended to represent a naive spatial model of catch rates,
 341 without knowledge of the spatial population dynamics.

342 4. Close area covering top 5 % of catch rates

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

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

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

350 4. Results

351 4.1. Emergent simulation dynamics

352 Individual habitat preferences and thermal tolerances result in different spa-
 353 tial habitat use for each population (Figure 2) and consequently different sea-
 354 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 rev-
 enue were experienced, as shown by Figure 4 (D), where several vessels tracks
 are overlaid on the revenue field, i.e.

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

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

361 *4.2. How does sampling-derived fisheries data reflect the underlying population* 362 *structure?*

363 The aggregated catch composition from each of the data sources over a ten-
 364 year period (which shows average seasonal patterns) at different spatial resolu-
 365 tions highlights different patterns in perceived community structure depending
 366 on the data source and aggregation level (Figure 5). The finer spatial grid for
 367 the true population (top left) and commercial data (top middle) show visually
 368 similar patterns, though there are large unsampled areas in the commercial data
 369 from a lack of fishing activity (particularly in the lower left part of the sam-
 370 pling domain). The survey data at this spatial resolution displays very sparse
 371 information about the spatial distributions of the populations. The slightly ag-
 372 gregated data on a 5 x 5 grid shows similar patterns and, while losing some of
 373 the spatial detail, there remains good consistency between the true population
 374 and the commercial data. Survey data starts to pick out some of the similar
 375 patterns as the other data sources, but lacks spatiotemporal coverage. The spa-
 376 tial catch information on a 10 x 10 and 20 x 20 grid lose a significant amount
 377 of information about the spatial resolutions for all data sources, and some dif-
 378 ferences between the survey, commercial and true population data emerge.

379
 380 Different perceptions of the proportion of each stock in an area are seen when
 381 we aggregate the data over a smaller geographical region at different timescales,
 382 with weekly (top), monthly (middle) and yearly (bottom) catch compositions
 383 from across an aggregated 20 x 20 area (Figure 6). In the true population, the
 384 monthly aggregation captures the major patterns of composition seen in the

385 weekly data with the percentage of different populations in the catch having
 386 similar mean and standard deviations. In the weekly data population 1 = 9.36
 387 (3.99), population 2 = 83.2 (5.60), population 3 = 3.57 (1.23), population 4 =
 388 3.91 (1.59); in the monthly data population 1 = 9.23 (3.87), population 2 = 83.3
 389 (5.52), population 3 = 3.62 (1.15), population 4 = 3.86 (1.52). While means
 390 were similar some of the variation was lost when aggregated to an annual level;
 391 population 1 = 9.90 (0.173), population 2 = 82.2 (0.308), population 3 = 3.82
 392 (0.119), population 4 = 4.03 (0.0502).

393
 394 The commercial data on a weekly basis shows some of the same patterns as
 395 the true population, though the population 1 (in red) is less well represented
 396 and some weeks are missing catches from the area. Here, weekly and monthly
 397 compositions were nearly identical, with monthly composition of population 1
 398 = 0.0472 (0.0139), population 2 = 94.4 (1.47), population 3 = 3.12 (1.47), pop-
 399 ulation 4 = 2.40 (0.444). Again, yearly values head a similar mean but smaller
 400 standard deviation.

401
 402 The survey data was only available on an annual basis, and showed again a
 403 slightly different composition; population 1 = 0.372 (0.00473), population 2 =
 404 87.7 (0.193), population 3 = 0.729 (0.0200), population 4 = 11.2 (0.172).

405 *4.3. How does data aggregation and source impact on spatial fisheries manage-* 406 *ment measures?*

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

412 The trend in fishing mortality for each species show that in most cases the
 413 fishery closure was successful in reducing fishing mortality on the species of in-
 414 terest (population 3; Figure 7), though interestingly the largest reductions in

415 fishing mortality happened immediately after the closures, following which the
416 fisheries “adapted” to the closures and fishing mortality increased again some-
417 what. The exception to the success was the closures implemented based on the
418 coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective
419 with all data sources. As expected, closures based on the “known” population
420 distribution were most effective, with differing degrees of success using the com-
421 mercial data. Fishing mortality rates on the other species changed in different
422 proportions, depending on whether the displaced fishing effort moved to areas
423 where the populations were found in greater or lesser density.

424

425 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))
426 highlights that the factor most contributing to differences in fishing mortality
427 before and after the closure was the population (72 % showing that the closures
428 were effective for population 3), followed by data resolution (21 %), data type
429 (7 %) with the least important factor the timescale (< 1 %). In general the finer
430 the spatial resolution of the data used the greater reduction in fishing mortality
431 for population 3 after the closures (Figure 8). The notable outliers are the com-
432 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
433 timescale, where closures were nearly as effective as the fine-scale resolution. In
434 this case the closures were sufficiently large to protect a core area of the habitat
435 for the population, but this was achieved in a fairly crude manner by closing a
436 large area - including area where the species was not found (Figure 9) that may
437 have consequences in terms of restricting the fishery in a much larger area than
438 necessary.

439

440 5. Discussion

441 Our study presents a new highly resolved fisheries simulation framework,
442 evaluates the importance of data scaling and considers potential bias introduced
443 through data aggregation when using fisheries data to infer spatiotemporal dy-

444 namics of fish populations. Understanding how fishers exploit multiple hetero-
 445 geneously distributed fish populations with different catch limits or conservation
 446 status requires detailed understanding of the overlap of resources; this is difficult
 447 to achieve using conventional modelling approaches due to species targeting in
 448 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
 449 ten data are aggregated or extrapolated which requires assumptions about the
 450 spatial and temporal scale of processes. Our study explores the assumptions
 451 behind such aggregation and preferential sampling to identify potential impacts
 452 on management advice. With modern management approaches increasingly
 453 employing more nuanced spatiotemporal approaches to maximise productivity
 454 while taking account of both the biological and human processes operating on
 455 different time-frames (Dunn et al., 2016), understanding assumptions behind
 456 the data used - increasingly a combination of logbook and positional informa-
 457 tion from vessel monitoring systems - is vital to ensure measures are effective.

459 *5.1. Simulation dynamics*

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

466 Our approach is unique in that it captures fine scale population and fish-
 467 ery dynamics and their interaction in a way not usually possible with real data
 468 and thus not usually considered in fisheries simulations. While other simulation
 469 frameworks seek to model individual vessel dynamics based on inferred dynam-
 470 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
 471 identify measures to meet particular management goals (Bailey et al., 2018), our
 472 framework allows users to explore the assumptions in modelling observational
 473 data and evaluate the underlying dynamics of such approaches at a fine spatial

474 and temporal scale. This offers the advantage that larger scale fishery patterns
475 are emergent properties of the system and results can be compared to those
476 obtained under a statistical modelling framework.

477

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

489

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

497

498 We take account of heterogeneity in fleet dynamics due to different prefer-
499 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an
500 individual vessel rather than fleet level. We do not explicitly define fleets as
501 rational profit maximisers at the outset, but consider there are several stages
502 to development of the fishery; information gathering through search where the
503 resource location is not known, followed by individual learnt behaviour of prof-
504 itable locations. This provides a realistic model of how fishing patterns are

505 established and maintained to exploit an uncertain resource through an explore-
506 exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

507 *5.2. How does sampling-derived fisheries data reflect the underlying population*
508 *structure?*

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

516
517 Our simulation shows that, despite biases introduced through the fishing
518 process, the commercially derived data could still inform on the key spatial
519 patterns in the community structures where the fisheries occurred, which was
520 spatially limited due to the “hotspots” of commercially valuable species be-
521 ing fished. Similarly, despite the even spatial coverage the survey was able to
522 capture some of the same spatial patterns as the true population, but missed
523 others due to gaps between survey stations limiting spatial and temporal cov-
524 erage (Figure 5). This provides a challenge when modelling unsampled areas in
525 inferring species distribution maps, though these limitations may be overcome
526 by understanding the relationship between the species and habitat covariates
527 where these are known at unsampled locations (Robinson et al., 2011).

528
529 *5.3. How does data aggregation and source impact on spatial fisheries manage-*
530 *ment measures?*

531 From our simulations spatial disaggregation was more important than the
532 temporal disaggregation of the commercial data. This reflects the fact that there
533 was greater spatial heterogeneity over the spatial domain than experienced in

individual locations over the course of the year (Figure 2).

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

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

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

565 these changes.

566 5.4. Model assumptions and caveats

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

571

572 Fish populations in our simulations move in pre-defined timescales and ac-
573 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).
574 Our assumptions in parameterising the model (movement rates, temperature
575 tolerances) will have a direct impact on our conclusions on the relative impor-
576 tance of spatial and temporal processes. These assumptions could be explored
577 in a future study by varying the parameters and assessing the robustness of our
578 conclusions. For our example application we have chosen movement rates to re-
579 flect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

580

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

589

590 5.5. Future applications of *MixFishSim*

591 We consider that the increased availability of high resolution catch and lo-
592 cational information from commercial fisheries will require it to be a key source
593 of data for ensuring management is implemented at the right scale in future.

For example, identifying hot-spots for bycatch reduction or identifying spatial overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al., 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the potential to test some of the assumptions behind the modelling approaches in identifying such hotspots and indeed behind spatiotemporal modelling in general (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical models under different data generation processes as exemplified by Stock et al. (2019)).

Other novel applications of our framework could be: testing different survey designs given multiple species and data generating assumptions (Xu et al., 2015); commercial index standardisation methods and approaches and understanding of appropriate scales and data aggregations and non-proportionality in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004); exploring assumptions about the distribution of natural mortality and fishing mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 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

623 potential biases that may be introduced when making inference on spatiotempo-
624 ral interactions will enable users to identify weaknesses in modelling approaches
625 and identity where data collection is needed to strengthen inference.

626

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

639

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

645

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

654 **Abbreviations**

655 Detail any unusual ones used.

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662 **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	-
$Tol_{c,wk,p}$	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
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
Le	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 (ordered by most effective first)

Scenario No	Population	F before	F after	% F change	data type	timescale	resolution
9	Population 3	1.08	0.29	-73.47	True Population	weekly	1.00
10	Population 3	1.08	0.29	-72.94	True Population	monthly	1.00
11	Population 3	1.08	0.35	-68.04	True Population	yearly	1.00
45	Population 3	1.08	0.58	-46.70	commercial	yearly	20.00
1	Population 3	1.08	0.58	-46.21	commercial	weekly	1.00
23	Population 3	1.08	0.59	-45.27	True Population	weekly	5.00
2	Population 3	1.08	0.59	-45.06	commercial	monthly	1.00
7	Population 3	1.08	0.60	-44.48	survey	yearly	1.00
24	Population 3	1.08	0.61	-43.20	True Population	monthly	5.00
3	Population 3	1.08	0.64	-40.82	commercial	yearly	1.00
25	Population 3	1.08	0.65	-39.94	True Population	yearly	5.00
17	Population 3	1.08	0.67	-38.11	commercial	yearly	5.00
15	Population 3	1.08	0.71	-34.38	commercial	weekly	5.00
43	Population 3	1.08	0.71	-34.31	commercial	weekly	20.00
16	Population 3	1.08	0.73	-32.58	commercial	monthly	5.00
51	Population 3	1.08	0.78	-27.92	True Population	weekly	20.00
37	Population 3	1.08	0.78	-27.76	True Population	weekly	10.00
39	Population 3	1.08	0.79	-26.98	True Population	yearly	10.00
38	Population 3	1.08	0.81	-25.47	True Population	monthly	10.00
21	Population 3	1.08	0.81	-25.21	survey	yearly	5.00
35	Population 3	1.08	0.81	-25.05	survey	yearly	10.00
44	Population 3	1.08	0.87	-19.91	commercial	monthly	20.00
52	Population 3	1.08	0.88	-18.39	True Population	monthly	20.00
30	Population 3	1.08	0.96	-11.06	commercial	monthly	10.00
29	Population 3	1.08	0.98	-9.80	commercial	weekly	10.00
31	Population 3	1.08	1.03	-4.36	commercial	yearly	10.00
53	Population 3	1.08	1.06	-1.64	True Population	yearly	20.00
49	Population 3	1.08	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; (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.

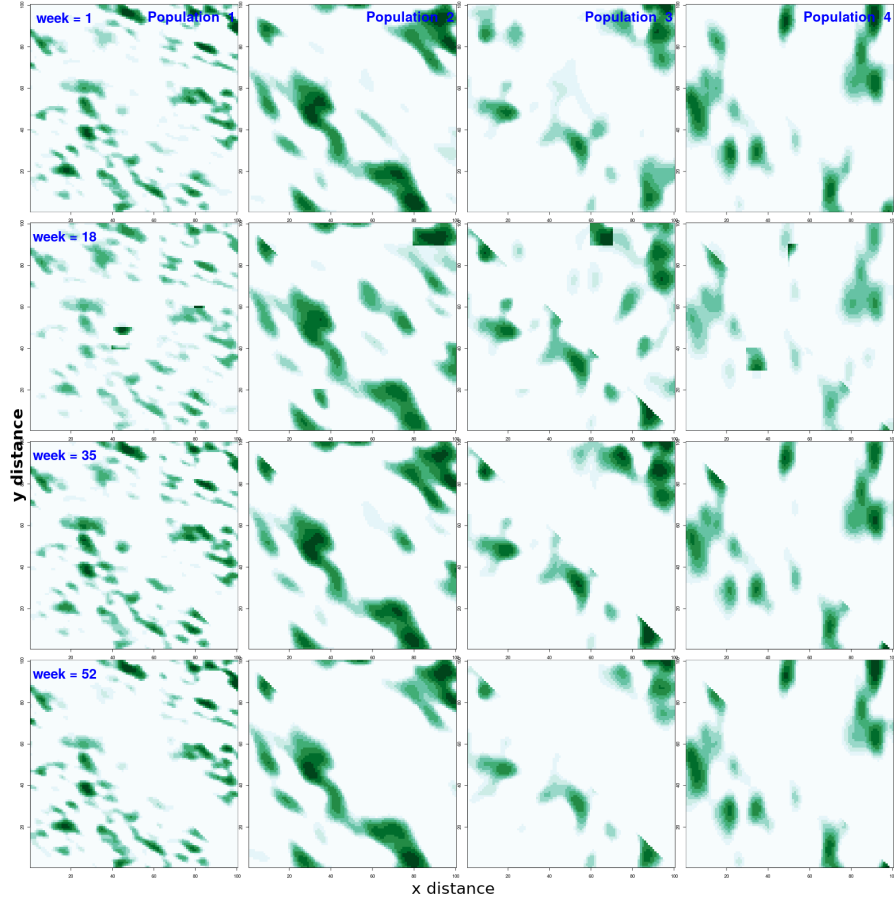


Figure 2: Spatial density (log abundance) for each of the four populations at four time steps. The darker the colour the greater the density of the population. Note that you can see the diagonal isotropic patterns in populations 2 and 3 and concentrated spawning areas in the second row of the panels ($t=18$).

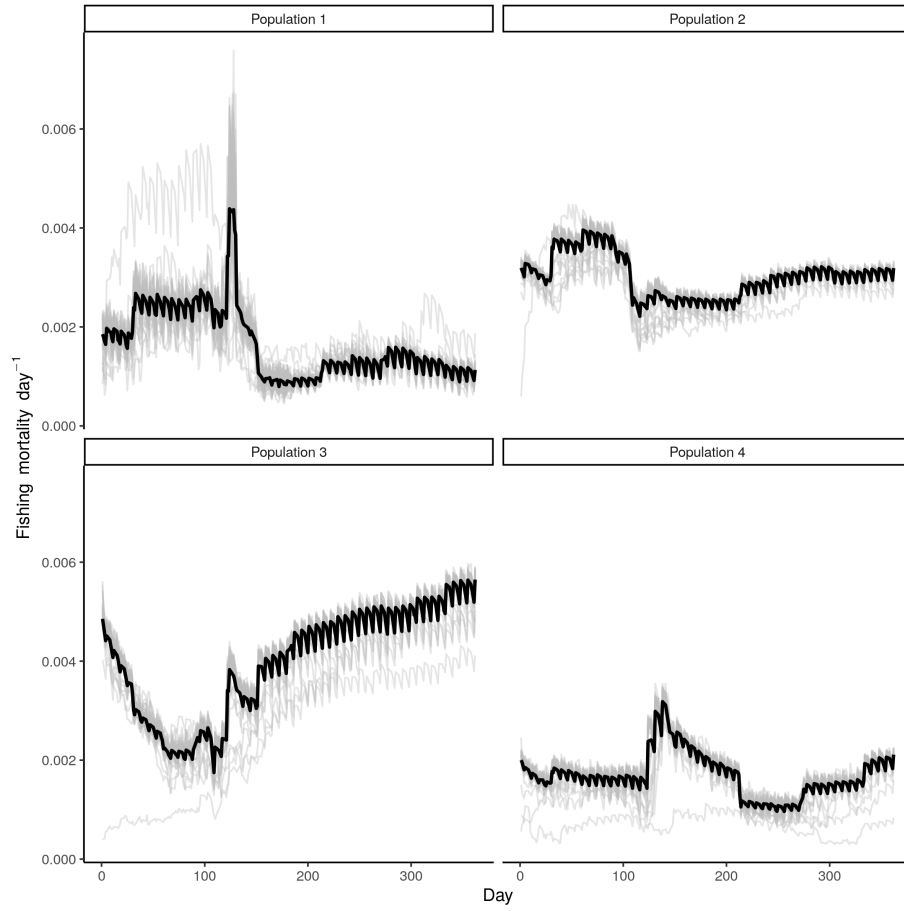


Figure 3: Fishing mortality dynamics - the daily fishing mortalities across the entire spatial domain showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line.

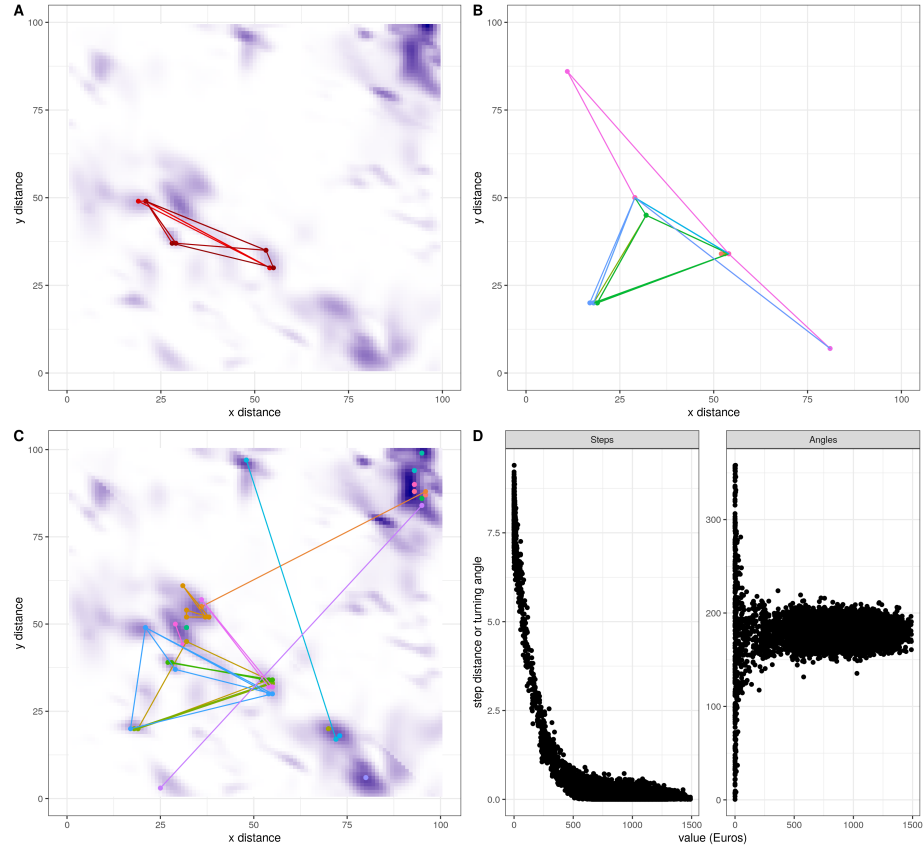


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (catch \times price); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that the field is wrapped on a torus so that distances between opposite side of the spatial domain are considered next to each other, hence apparent large movements; (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.

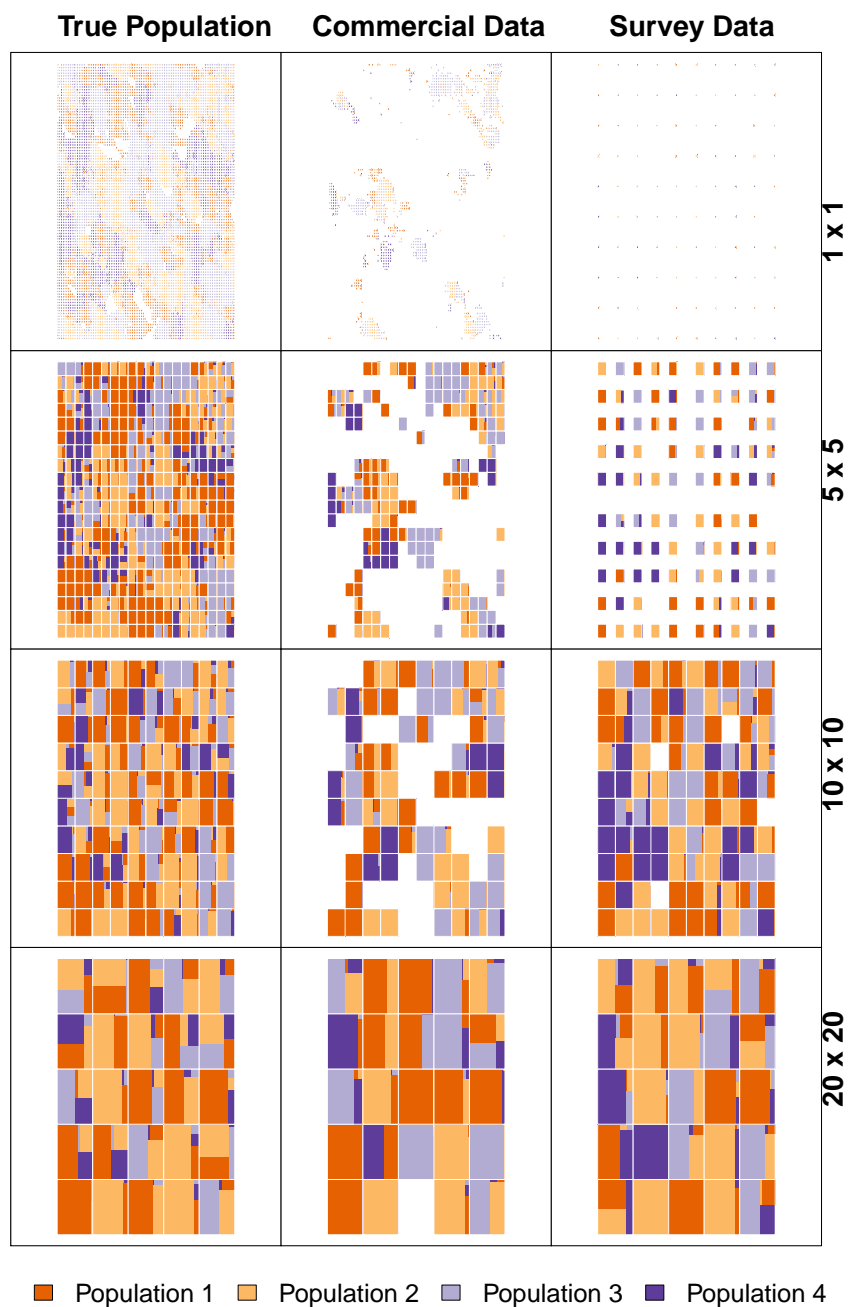


Figure 5: Data aggregation at different spatial resolutions over a ten year period.



Figure 6: 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.

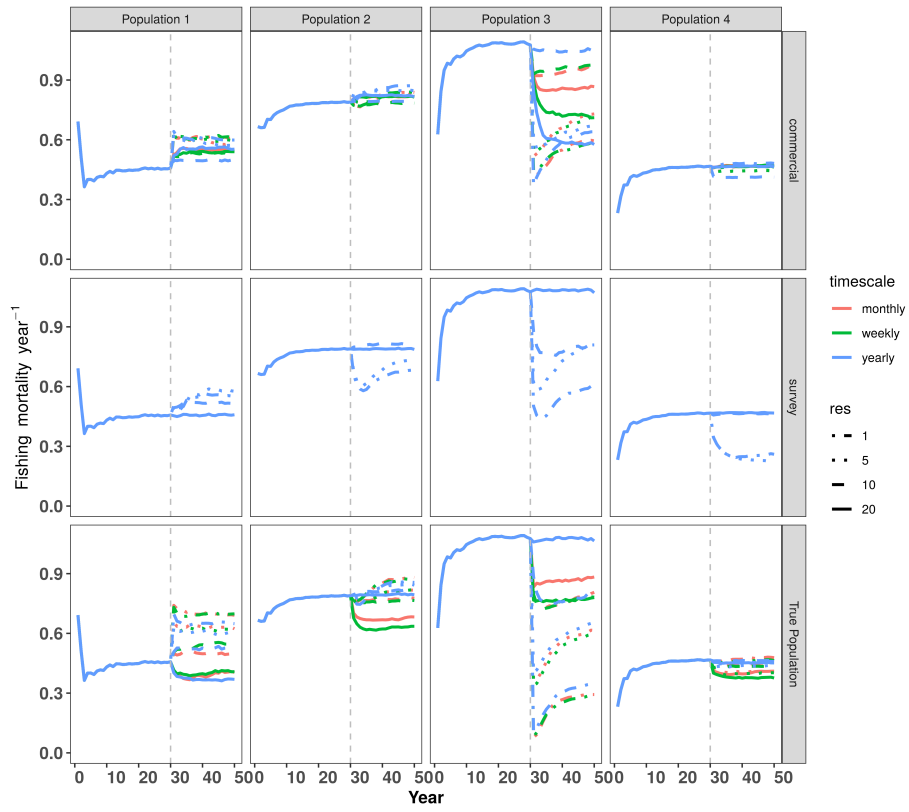


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.



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



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

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