

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 and moving fish populations, and iii) fishery dynamics for multiple fleet characteristics based on population targeting under an explore-exploit strategy.

We applied *MixFishSim* to infer community structure when using data generated from: commercial catch, a fixed-site sampling survey design and the true (simulated) underlying populations. We thereby establish the potential limitations of fishery-dependent data in providing a robust characterisation of spatiotemporal distributions. Different spatial patterns were evident and the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. A simulated area closure showed that aggregation across time periods has less of a negative impact on the closure success than aggregation over space. While not as effective as when based on the true population,

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closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.

Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal resolutions. From our application we conclude that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

Keywords: spatiotemporal, mixed fisheries, individual based, spatial management, heterogeneity, bycatch avoidance

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1. Introduction

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

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch which is often discarded (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019). Adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2015; Dunn et al., 2014). However, if fisheries are to reduce unwanted catch through

18 ~~spatial avoidance, an in-depth understanding of spatiotemporal fishery dynam-~~
19 ~~ics is required.~~

20

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

33

34

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

44

45 More refined spatiotemporal information has since become available through
46 the combination of logbook and Vessel Monitoring System (VMS) data (Lee
47 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2017)
48 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 have 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 sources of sampling-derived fisheries data reflect the underlying community structure?
2. How do 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 to test if these are a true reflection of the relative density of the populations. We then iii) simulate a fishery closure to protect a species based on different spatial and temporal data aggregations.

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 characteristics of the different processes (Figure 1). Sub-
86 modules to capture the full system comprised: 1) population dynamics, 2) re-
87 cruitment dynamics, 3) population movement, 4) fishery dynamics.

88
89 Population dynamics for any number of species, as chosen by the user, oper-
90 ate on a daily time-step (with recruitment occurring only during defined seasons
91 for each population), while population movement occurs on a weekly time-step,
92 with the fishing module operating on a tow-by-tow basis (i.e., multiple events a
93 day).

95 2.1. Population dynamics

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

all parameter details):

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

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

112

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

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

where $C_{c,d}$ is the summed catch from the fishing model across all fleets and vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass for the population in the cell. Here, catch is the sum of those across all fleets and vessels, $C_{c,d} = \sum_{fl=1}^{FL} \sum_{v=1}^{V_{fl}} E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$ with fl and FL the fleet and total number of fleets, v and V_{fl} the vessel and total number of vessels per fleet 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.

124

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):

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

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

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 Ricker form (Ricker, 1954) is:

$$\bar{R}_{c,d} = B_{c,d} \cdot e^{(\alpha - \beta \cdot B_{c,d})} \quad (4)$$

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

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

2.3. Population movement dynamics

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

The combined process results in a population structure and movement pattern unique to each population, with population movement occurring on a weekly basis. Modeling population movement on a weekly timescale reflects that fish tend to aggregate in species-specific locations observed to last between one and two weeks (Poos and Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts in fish populations 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 contains the expo-
 161 nential and double exponential as special cases and it enables us to model the
 162 spatial autocorrelation observed in animal populations where density is more
 163 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and Ri-
 164 jnsdorp, 2007b). We change the parameters to implement different spatial struc-
 165 tures for the different populations using the *RandomFields* R package (Schlather
 166 et al., 2015). We define a stationary habitat field with an anisotropic pattern
 167 (to simulate a depth gradient) and combine it with a temporally dynamic ther-
 168 mal tolerance field to imitate two key drivers of population dynamics without
 169 modelling the processes explicitly. Each population was initialised at a single
 170 location, and subsequently moved across the entire space according to a proba-
 171 bilistic distribution based on habitat suitability (represented by the normalised
 172 values from the GRFs), temperature tolerance and distance from current cell:

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

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

177
 178 During pre-defined weeks of the year the habitat suitability is modified with
 179 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.

183

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

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

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 the mean and standard deviation of the population temperature tolerance (see Table 2 for variable descriptions)..

192

193 2.4. Fleet dynamics

Fleet dynamics were broadly categorised into three components. *Fleet targeting* determined the fleet catch efficiency and preference towards a particular population; *trip-level decisions* determined the initial location to be fished at the beginning of a trip; and *within-trip decisions* determined fishing locations within a trip. This results in an explore-exploit strategy 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.

205 2.4.1. Fleet targeting

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

213 2.4.2. Decision about where to fish at the start of a trip

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

224 2.4.3. Decision about where to fish within a trip

225 Fishing locations within a trip are initially determined by a modified ran-
226 dom walk process. As the simulation progresses the within-trip decision become
227 gradually more influenced by experience gained from past fishing locations (as
228 per the initial trip-level location choice), moving location choice towards areas
229 of higher perceived profit. A random walk was chosen for the exploratory fishing
230 process as it is the simplest assumption commonly used in ecology to describe
231 optimal animal search strategy for exploiting heterogeneously distributed prey
232 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-
233 dom walk, movement is a stochastic process through a series of steps. These

234 steps have a length, and a direction that can either be equal in length or take
 235 some other functional form. The direction of the random walk was also cor-
 236 related (known as ‘persistence’) providing some overall directional movement
 237 (Codling et al., 2008).

238

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

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

245 where $L_{c,d,p}$ is landings of a population p , and Pr_p price of a population. All
 246 population prices were kept the same across fleets and seasons. Here, when
 247 fishing is successful vessels remain in a similar location and continue to exploit
 248 the local fishing grounds. When unsuccessful, they move some distance away
 249 from the current fishing location. The movement distance retains some degree
 250 of stochasticity, that can be controlled separately, but is determined by the re-
 251 lationship: ([CM: use ln where we use the natural logarithm. Double-check this
 252 equation is right as per the code. As it looks different here: https://github.com/pdolder/MixFishSim/blob/master/R/step_length.R]. There it looks to
 253 simplify to $b_2(b_1/b_2)^{Rev/b_3}$, assuming parameters are positive.)
 254

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

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

257 by:

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

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

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

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

264 2.4.4. Local population depletion

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

274 2.5. Fisheries-independent survey

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

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

282

283 2.6. Software: R-package development

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

287

288 3. Model calibration

289 We calibrate *MixFishSim* to investigate the influence of data aggregation on
290 spatial inference.

291 3.1. Population models

292 We calibrated the simulation model for four example populations with dif-
293 ferent demographics, growth rates, natural mortality and recruitment (Table
294 4). Habitat preference (Figure S7) and temperature (Figures S9, with tem-
295 perature tolerance S10) defined to be unique to each population resulting in
296 differently weekly distribution patterns (Figures S1-S3). In addition, each of
297 the populations was assumed to have two defined spawning areas that result in
298 the populations moving towards these areas in pre-defined weeks (Figure S8)
299 with population-specific movement rates (Table 4). The population demograph-
300 ics were chosen to broadly represent three mobile low-medium value groundfish
301 species and one high value species with low mobility, with the dynamics hypo-
302 thetical but might be expected in a typical demersal fishery.

303 3.2. Fleet calibration

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

307 hence different spatial dynamics. The learned random walk process implies that
 308 within a fleet different vessels have different spatial distributions based on in-
 309 dividual experience. The step function was calibrated dynamically within the
 310 simulations as the maximum revenue obtainable was not known beforehand.
 311 This was implemented so that vessels take smaller steps when fishing at a loca-
 312 tion that yields landings value in the top 90th percentile of the value experienced
 313 in that year so far (as defined per fleet in Table 5).

314

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

324

325 *3.3. Survey settings*

326 The survey simulation was set up with a fixed gridded station design with
 327 100 stations fished each year, starting on day 92 and ending on day 112 (5
 328 stations per day) with same catchability parameter ($Q_p = 1$) for all populations.
 329 This approximates a real world survey design with limited seasonal and spatial
 330 coverage.

331 *3.4. Example research question*

332 To illustrate the capabilities of *MixFishSim*, we investigate the influence of
 333 the temporal and spatial resolution of different data sources on the reduction in
 334 catches of a population given spatial closures. To do so, we set up a simulation
 335 to run for 50 years based on a 100×100 square grid (undetermined units), with

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

339

340 *How does sampling-derived fisheries data reflect the underlying population*
341 *structure?*

342

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

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

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

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

354

355 The following steps are undertaken to determine closures:

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

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

- 364 • **data types:** commercial logbook data, survey data and true population,
- 365 • **temporal resolutions:** weekly, monthly and yearly closures,
- 366 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,

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

376 4. Results

377 4.1. Emergent simulation dynamics

378 Individual habitat preferences and thermal tolerances result in different spa-
379 tial habitat use for each population (Figure S5) and consequently different sea-
380 sonal exploitation patterns (Figure S6).

381 It can be seen from a single vessels movements during a trip that the vessel
382 exploits three different fishing grounds, each of them multiple times (Figure 2A),
383 while across several trips fishing grounds that are further apart are fished (Figure
384 2B). These different locations relate to areas where the highest revenue were
385 experienced, as shown by Figure 2D, where several vessels tracks are overlaid
386 on the revenue field.

387 Vessels from the same fleet (and therefore targeting preference) may exploit
388 some shared and some different fishing grounds depending on their own personal
389 experience during the exploratory phase of the fishery (Figure 2 (C)). This

390 results from the randomness in the correlated random walk step function, with
391 distance moved during the exploitation phase and the direction stochastically
392 related to the revenue experienced on the fishing ground (Figure 2 (D)).

393 *4.2. How does sampling-derived fisheries data reflect the underlying population*
394 *structure?*

395 Catch composition aggregated at different spatial resolutions from each of
396 the data sources (average seasonal patterns over a ten-year period) highlights dif-
397 ferent patterns in perceived community structure depending on the data source
398 and aggregation level (Figure 3). The finer spatial grid for the true popula-
399 tion (top left) and commercial data (top middle) show visually similar patterns,
400 though there are large unsampled areas in the commercial data from a lack
401 of fishing activity (particularly in the lower left part of the sampling domain).
402 Survey data at this spatial resolution displays very sparse information about
403 the spatial distributions of the populations. The slightly aggregated data on a
404 5 x 5 grid shows similar patterns and, while losing some of the spatial detail,
405 there remains good consistency between the true population and the commercial
406 data. Survey data starts to pick out some of the similar patterns as the other
407 data sources, but lacks spatiotemporal coverage. The spatial catch information
408 on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the
409 spatial resolutions for all data sources, and some differences between the survey,
410 commercial and true population data emerge.

411
412 Different perceptions of the proportion of each stock in an area are seen when
413 we aggregate the data at different timescales, with weekly (top), monthly (mid-
414 dle) and yearly (bottom) catch compositions from across an aggregated 20 x 20
415 area showing different patterns (Figure 4). In the true population, the monthly
416 aggregation captures the major patterns of composition seen in the weekly data
417 with the percentage of different populations in the catch having similar mean
418 and standard deviations (Table 7). In the weekly and monthly data population
419 2 dominates. However, some of the variation was lost when aggregated to an

420 annual level, as indicated from the lower standard deviations (Table 7).

421

422 Weekly commercial data shows some of the same patterns as the true popu-
423 lation, though population 1 is less well represented and some weeks are missing
424 catches from the area. Here, weekly and monthly compositions were nearly
425 identical (Figure 4; Table 7). Yearly values had a similar mean but smaller
426 standard deviation. The survey data was only available on an annual basis, and
427 showed again a slightly different composition from the true population and the
428 commercial data; in particular a greater proportion of population 4 (Figure 4).

429 *4.3. How does data aggregation and source impact on spatial fisheries manage-*
430 *ment measures?*

431 In most cases the fishery closure was successful in reducing fishing mortality
432 on the species of interest (population 3; Figure 5). Interestingly the largest re-
433 ductions in fishing mortality happened immediately after the closures, following
434 which the fisheries “adapted” to the closures by finding new areas of high abun-
435 dance to fish. This led to fishing mortality increasing again, though not to past
436 levels (Figure 5). The exception to the success was the closures implemented
437 based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that
438 was ineffective (i.e. failed to reduce fishing mortality) with all data sources.
439 As expected, closures based on the “known” population distribution were most
440 effective, with differing degrees of success using the commercial data. Fishing
441 mortality rates on the other species changed in different proportions, depending
442 on whether the displaced fishing effort moved to areas where the populations
443 were found in greater or lesser density.

444

445 The factor most contributing to differences in fishing mortality before and
446 after the closure was the population (72 % showing that the closures were effec-
447 tive for population 3), followed by spatial data resolution (21 %), data type (7
448 %) with the least important factor the timescale (< 1 %). In general the finer
449 the spatial resolution of the data used the greater reduction in fishing mortality

450 for population 3 after the closures (Figure 6). The notable outliers are the com-
 451 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
 452 timescale, where closures were nearly as effective as the fine-scale resolution. In
 453 this case the closures were sufficiently large to protect a core area of the habitat
 454 for the population, but this was achieved in a fairly crude manner by closing a
 455 large area - including area where the species was not found (Figure 7) that may
 456 have consequences in terms of restricting the fishery in a much larger area than
 457 necessary. We found that these trade-offs existed, with high catches maintained
 458 with an effective closure when the highest resolution data was used, with the
 459 effect being linear when the true population distribution was known and also
 460 persisting for closures based on commercial information (Figure 8).

462 5. Discussion

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

tion from vessel monitoring systems - is vital to ensure measures are effective.

5.1. *Simulation dynamics*

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

Our approach is unique in that it captures fine scale population and fishery dynamics and their interaction in a way not usually possible with real data and thus not usually considered in fisheries simulations. While other simulation frameworks seek to model individual vessel dynamics based on inferred dynamics from VMS and logbook records (Bastardie et al., 2010), or as a system to identify measures to meet particular management goals (Bailey et al., 2019), our framework allows users to explore assumptions in modelling observational data and to evaluate the underlying dynamics of such approaches at fine spatial and temporal scales. This offers the advantage that larger scale fishery patterns are emergent properties of the system and results can be compared to those obtained under a statistical modelling framework.

Typically, simulation models that treat fish as individuals are focussed on exploring the inter- and intra- specific interactions among fish populations (e.g. OSMOSE; Shin et al. (2004)) in order to understand how they vary over space and time. Our focus was on understanding the strengths and limitations of inference from catch data obtained through commercial fishing activity with fleets exploiting multiple fish populations. This shows how realised catch distributions may differ from the underlying populations, as identified by Gillis et al. (2008). As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014) taking account of environmental but not demographic

509 stochasticity, while incorporating detailed fishing dynamics that take account
510 of different drivers in a mechanistic way.

511

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

519

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

529 *5.2. How does sampling-derived fisheries data reflect the underlying population* 530 *structure?*

531 Our results demonstrate the importance of considering data scale and resolu-
532 tion when using observational data to support management measures. We find
533 that understanding of the community composition dynamics will depend on the
534 level of data aggregation and its important to consider the scale of processes;
535 including population movement rates, habitat uniformity and fishing targeting
536 practices if potential biases in data are to be understood and taken into account
537 (Figures 2 and S5).

538

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 even spatial coverage the survey captured 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 3). 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).

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

From our simulations spatial disaggregation was more important than the temporal disaggregation of the commercial data. This reflects the fact that there was greater spatial heterogeneity over the spatial domain than experienced in given locations over the course of the year (Figure S5).

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 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

569 have the potential to reduce fishing mortality. The likely cost of poor spatial
570 and temporal resolution is associated with reduced effectiveness and potentially
571 closing fishing opportunities for other fisheries (Figure 8).

572

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

582

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

588 5.4. *Model assumptions and caveats*

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

593

594 Fish populations in our simulations move in pre-defined timescales and ac-
595 cording to fixed habitat preferences and temperature gradients (Figures S7, S9).
596 Our assumptions in calibrating the model (movement rates, temperature toler-
597 ances) will have a direct impact on our conclusions on the relative importance
598 of spatial and temporal processes. These assumptions could be explored in a

future study by varying the parameters and assessing the robustness of our conclusions. For our example application we have chosen movement rates to reflect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

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

5.5. Future applications of *MixFishSim*

We consider that the increased availability of high resolution catch and locational information from commercial fisheries will make it a key source 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., 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the potential to test some of the assumptions behind the modelling approaches in identifying such hotspots and indeed behind spatiotemporal modelling in general, e.g. comparing GAMs, GLMMs, Random Forests and geostatistical models under different data generation processes as exemplified by Stock et al. (2019).

Other novel applications of our framework could be: testing different survey designs given multiple species and data generating assumptions (Xu et al., 2015); commercial index standardisation methods and approaches and understanding of appropriate scales and data aggregations and non-proportionality in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);

exploring assumptions about the distribution of natural mortality and fishing mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 2014); at-sea sampling scheme designs to deliver unbiased estimates of population parameters (Cotter and Pilling, 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn et al., 2016); testing the ability of commonly employed fleet dynamics models such as Random Utility Models to capture fine scale dynamics and understand their importance (Girardin et al., 2017); and as a detailed operating model in a management strategy evaluation (Mahévas and Pelletier, 2004).

6. Conclusions

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

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

658 negative effect on the effectiveness of the measures though, importantly, there
659 was still some benefit even with coarse spatial resolution.

660

661 While case-specific, our findings emphasise the need to understand popu-
662 lation demographics, habitat use and movement rates in designing any closure
663 scenario based on observational sampling. This information can then be used
664 to set the bounds on data aggregation used in modelling studies aimed at in-
665 forming the management measures.

666

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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
$F_{c,d}$	Rate of fishing mortality in cell c on day d	d^{-1}
$M_{c,d}$	Rate of natural mortality in cell c on day d	d^{-1}
$B_{c,d}$	Biomass in cell c on day d	kg
Recruitment dynamics		
$\tilde{R}_{c,d}$	is the number of fish recruited in cell c for day d	d^{-1}
α	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	number fish
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	number fish

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	$\text{€}.\text{kg}^{-1}$
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 landings value n th quantile	90	90	85	90	80
step function $rate$	20	30	25	35	20
Past Knowledge = TRUE					
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

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

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

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

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

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

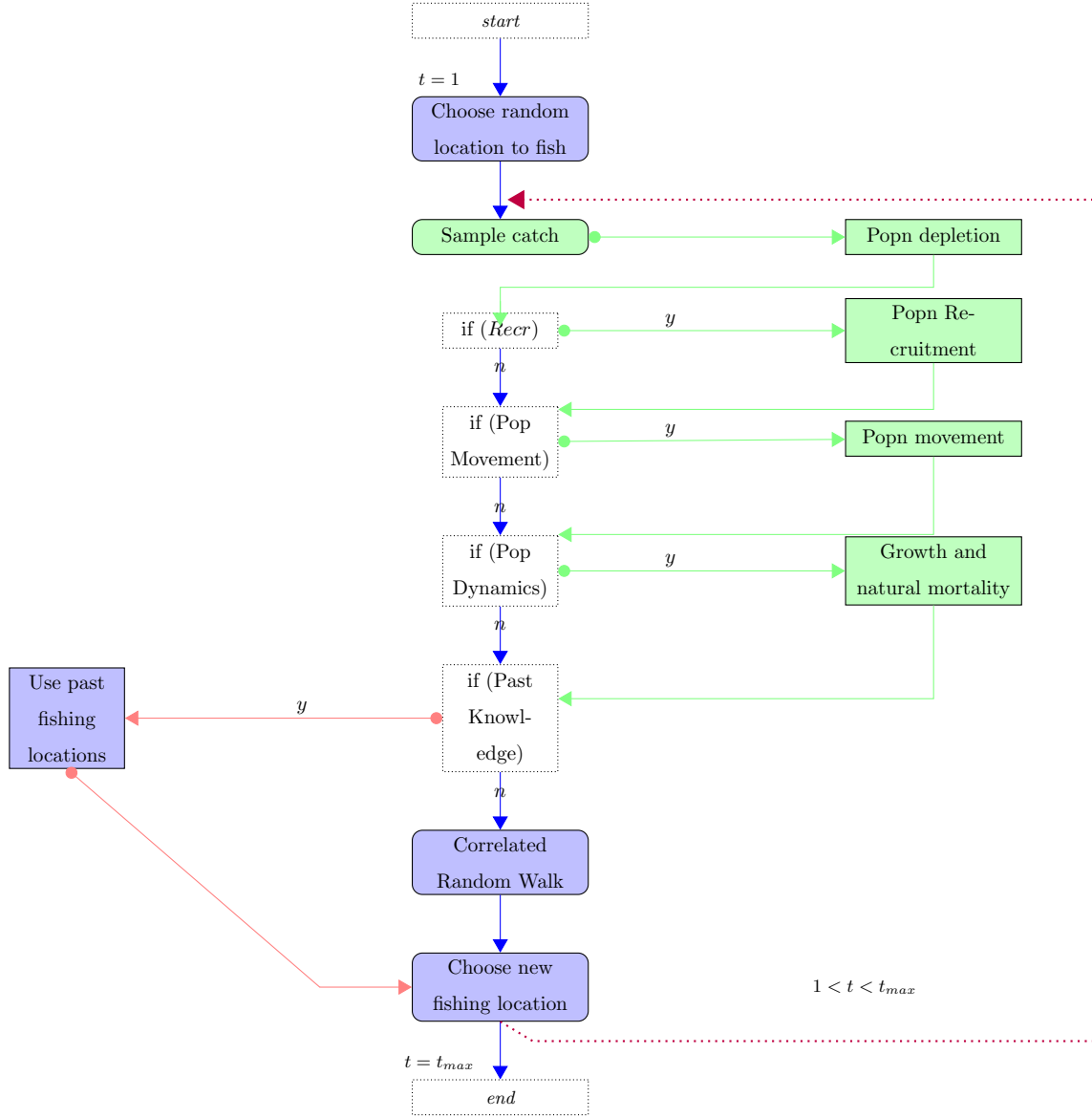


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Recr), (Pop Movement), (Pop Dynamics)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

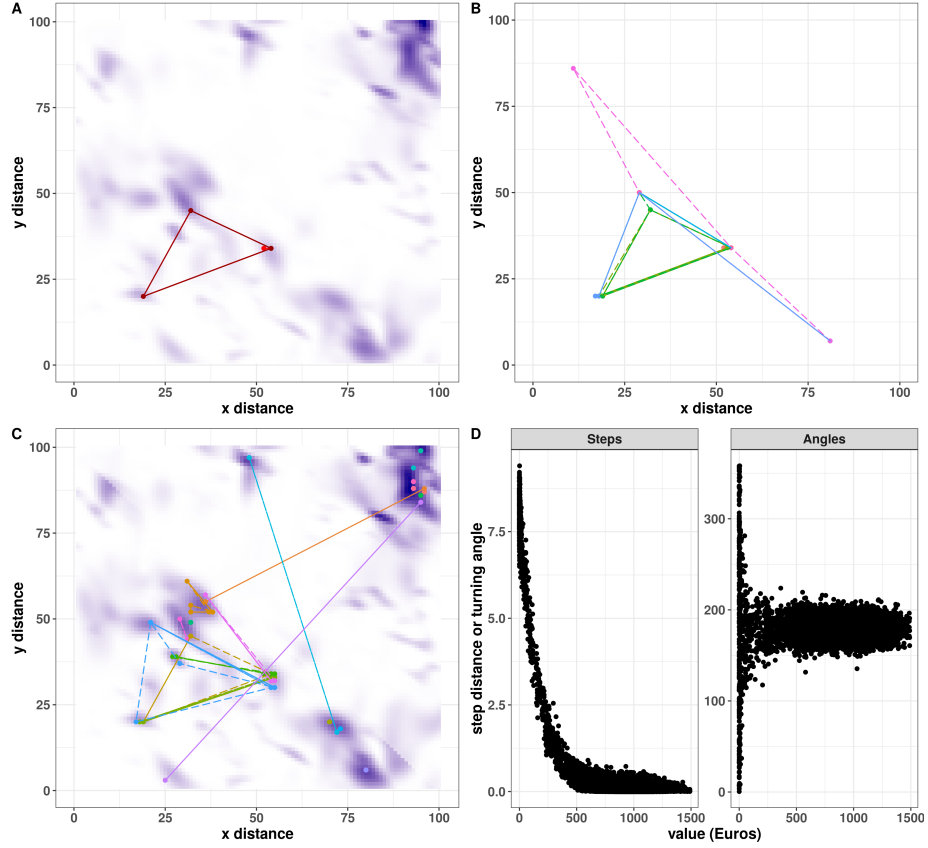


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are a mixture of correlated random walk (solid lines) and experience-based (dashed lines), and that the field is wrapped on a torus so that opposite sides of the spatial domain are considered spatially close; (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation.

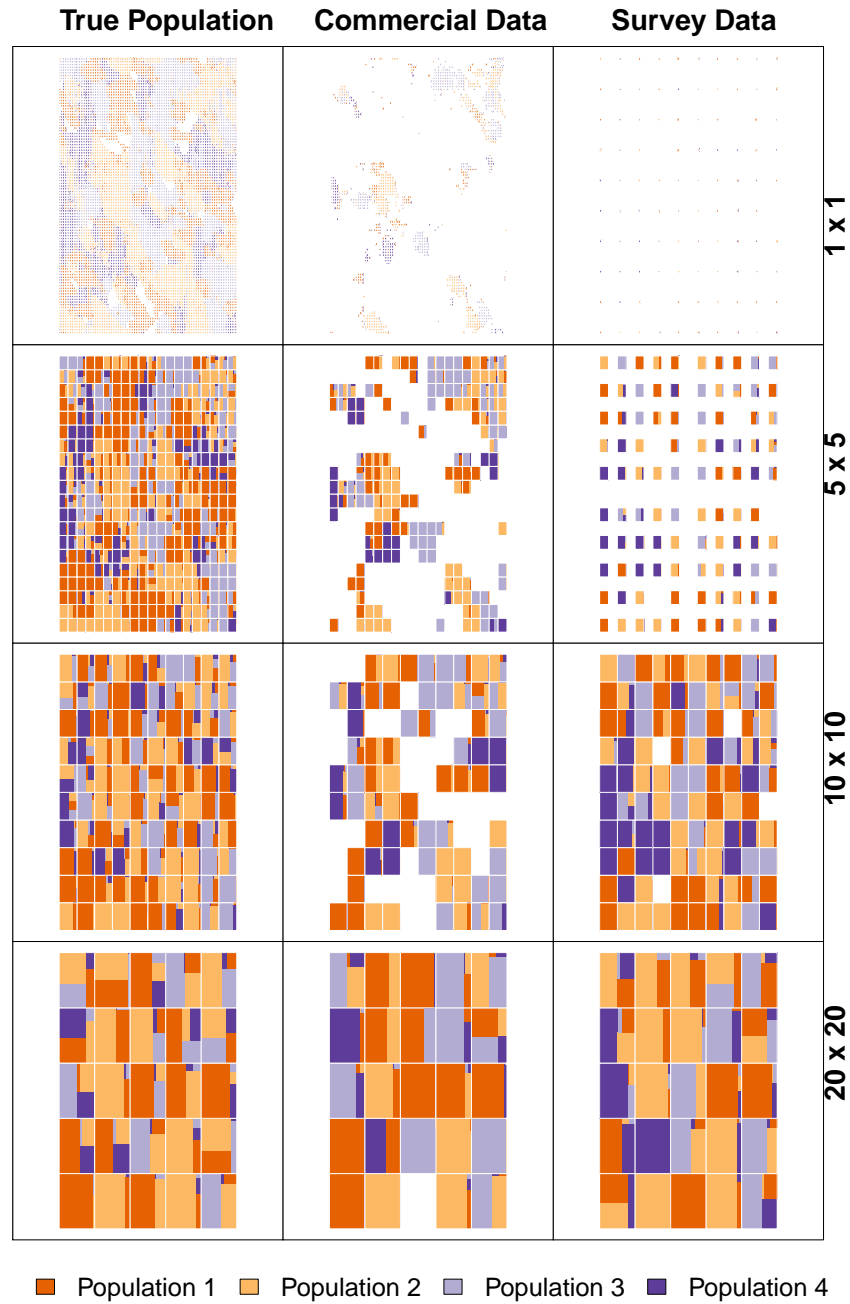


Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit. Figure produced using the R package ‘mapplots’ (Gerritsen (2014)).

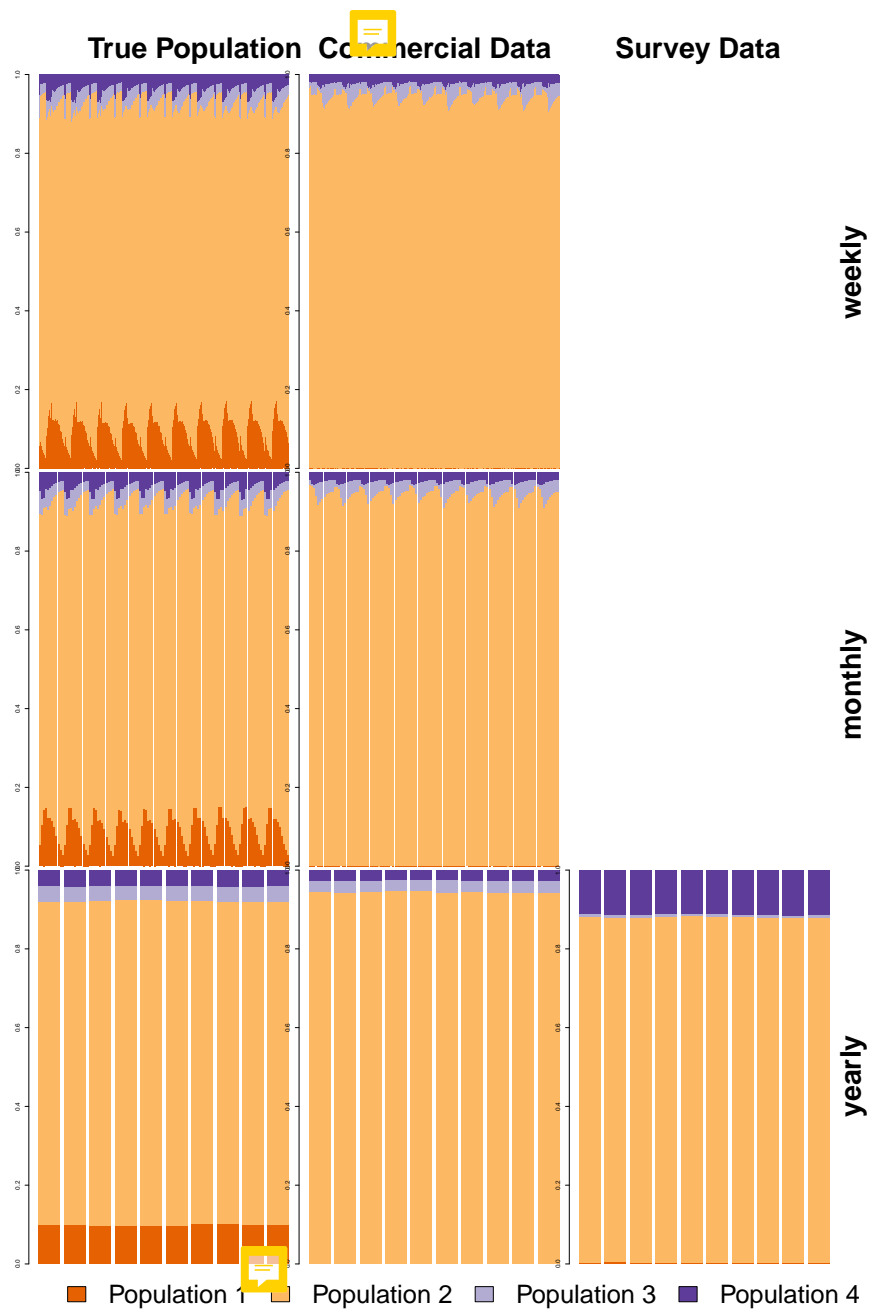


Figure 4: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

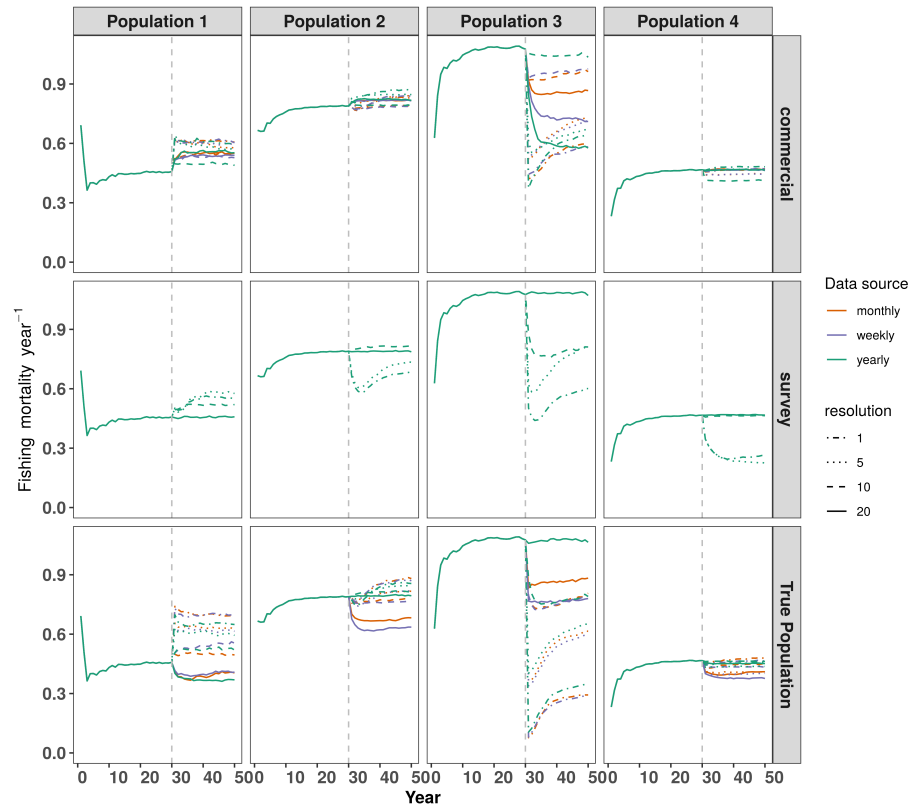


Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

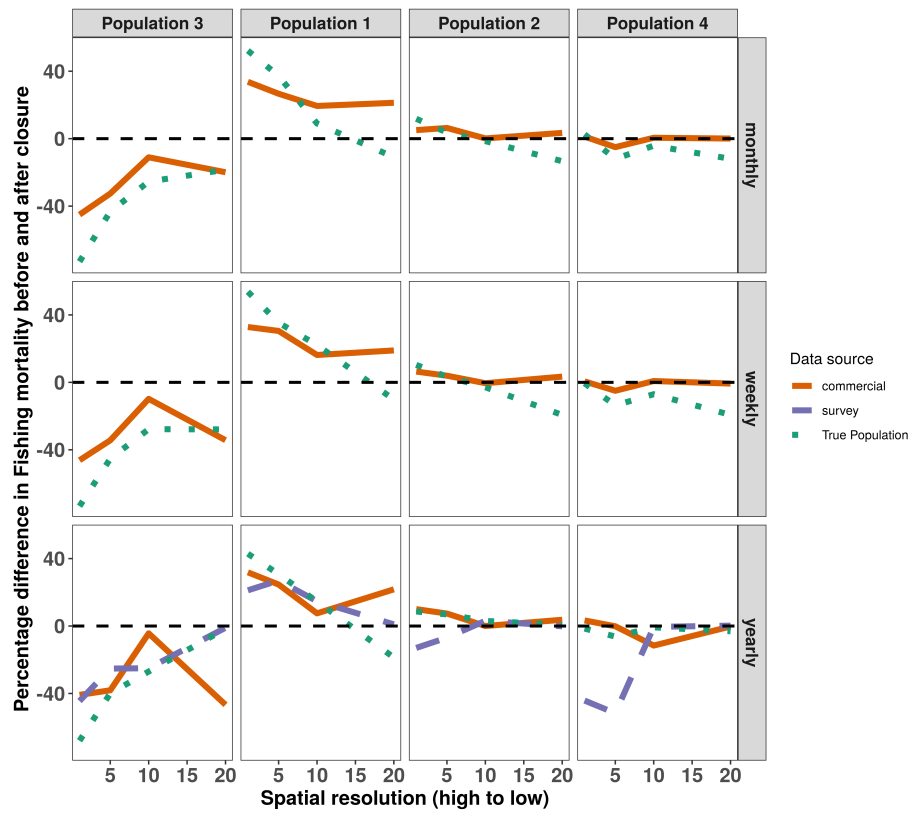


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

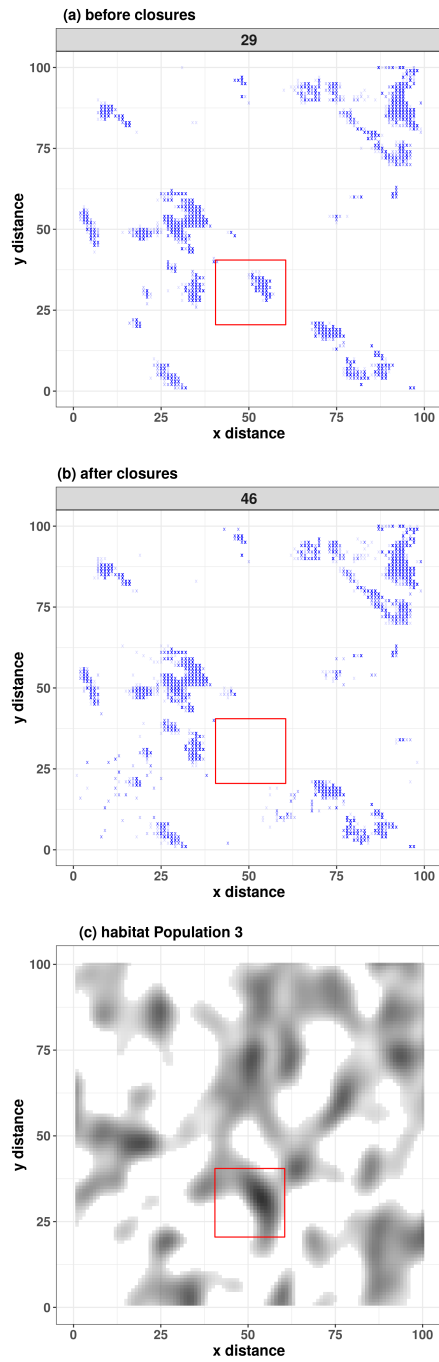


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

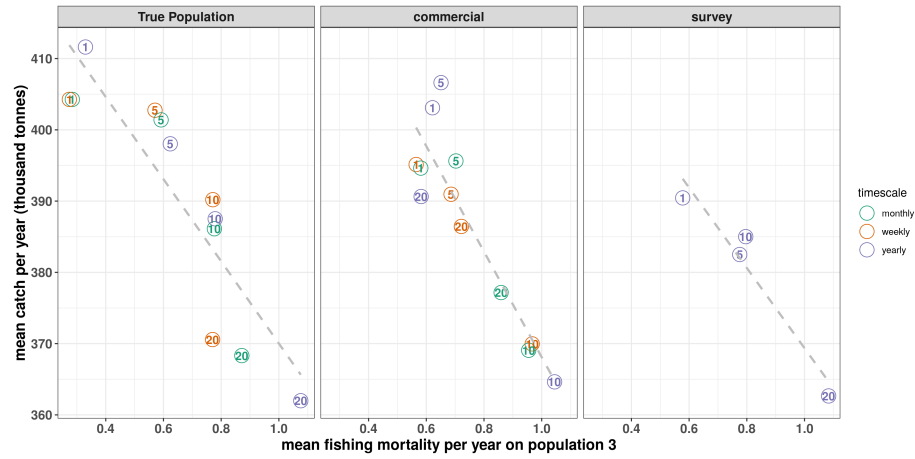


Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the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



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