

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

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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, 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. Fishers generally only have partial knowledge of species distributions and so limited control over what species they select when fishing in ‘mixed fisheries’. This results in catches of vulnerable species and species with low-quota. These species may be thrown overboard in a process called discarding and discarding catches that are not recorded leads to biased perception of the effects of fisheries on ecosystems. Ultimately the unaccounted discards limit our ability to control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage biological and economic sustainability of fisheries (Ulrich et al., 2011; Batsleer et al., 2015).

There is increasing interest in technical solutions such as gear adaptations and spatial closures as measures to reduce discarding of unwanted catches (Ken-

nelly and Broadhurst, 2002; Catchpole and Reville, 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, to reduce unwanted catch through spatial measures requires an in-depth understanding of the spatiotemporal dynamics of the fishery.

Effective spatial management requires implementation at appropriate spatial scales. These spatial scales shape the trade-offs between protection of populations and economic impacts on fisheries (Dunn et al., 2016). In mixed fisheries, the problem is to identify a scale that promotes species avoidance for vulnerable or low-quota species while allowing continuance of sustainable fisheries for available quota species. Identifying the appropriate spatial scale remains challenging because collecting data on fish distribution at high temporal and spatial resolutions is expensive and difficult. Proxies for the spatial distributions are usually inferred from fisheries-dependent data or from fisheries-independent data. Fisheries-dependent data includes all data on catch and effort from commercial fishing operations while fisheries-independent data includes data collected on board scientific research vessels.

Inferences on fish distributions are hampered where spatial and temporal information is coarse. Sampling designs for scientific research vessel surveys generally aim for unbiased estimates of local abundance. However, high costs of these surveys generally results in restrictions in terms the number of samples. As a result, sampling is usually restricted to a few weeks a year, and sampling stations are usually coarsely spaced. Moreover, the gear chosen for the survey determines the selectivity for certain species and size classes within fish communities. This selectivity determines the usefulness of relative occurrence in survey catches as proxies for abundances in the fish communities.

Proxies for spatial distribution derived from commercial fisheries in theory

allow for much larger sample sizes. These commercial fisheries are often at sea throughout the year, making many fishing hauls. However, spatial information from fisheries is often limited because data on catch and effort is collected or aggregated across larger gridded areas (Branch et al., 2005). If spatially aggregated data does not allow identification of spatial features it may lead to poorly designed spatial management measures that are ineffectual or have unintended consequences (Costello et al., 2010; Dunn et al., 2016). 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).

Even where high-resolution spatiotemporal information is available (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2017, see e.g.) commercial catch per unit of effort may still be biased because of fisheries dynamics. 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 inherently biased sampling where target species are over-represented in the catch because fishers exploit areas of high abundance. For effective adaptive spatial management the effects of spatiotemporal aggregation in data and fishery targeting need to be understood.

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?

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

89
90 We use these evaluations to draw inference on the utility of commercial data
91 in supporting management decisions.

92 **2. Materials and Methods**

93 A Discrete-event simulation (DES) model of a hypothetical fishery was de-
94 veloped as a software package (*MixFishSim*). The modular approach enabled
95 efficient computation by allowing for sub-modules implemented on time-scales
96 appropriate to capture characteristics of the different processes (Figure 1). Sub-
97 modules to capture the full system comprised: 1) population dynamics, 2) re-
98 cruitment dynamics, 3) population movement, 4) fishery dynamics.

99
100 Population dynamics for any number of species, as chosen by the user, oper-
101 ate on a daily time-step (with recruitment occurring only during defined seasons
102 for each population), while population movement occurs on a weekly time-step,
103 with the fishing module operating on a tow-by-tow basis (i.e., multiple events a
104 day).

105

106 2.1. Population dynamics

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

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

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

123

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

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

128 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and
 129 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.

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 adja-
 cent cells, and random (diffusive) movement, governed by a stochastic process
 where movement between adjacent cells is described by a set of probabilities.

153 Stochastic probabilities are affected by the suitability of habitat, temperature
154 in a cell and the thermal tolerance of a population to that temperature.

155

156 The combined process results in a population structure and movement pat-
157 tern unique to each population, with population movement occurring on a
158 weekly basis. Modeling population movement on a weekly timescale reflects
159 that fish tend to aggregate in species-specific locations observed to last between
160 one and two weeks (Poos and Rijnsdorp, 2007b). Therefore this process ap-
161 proximated the demographic shifts in fish populations throughout a year with
162 seasonal spawning patterns (Figure S1).

163

164 To simulate fish population distribution in space and time a Gaussian spa-
165 tial process was employed to model habitat suitability for each of the popula-
166 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
167 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
168 $\{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,
169 where the correlation strength weakens with distance controlled by two param-
170 eters, with ν a scale parameter in the units of distance and κ a shape parameter
171 which determines the smoothness of the process. We use the most commonly
172 used Matérn covariance structure as it is a flexible form that contains the expo-
173 nential and double exponential as special cases and it enables us to model the
174 spatial autocorrelation observed in animal populations where density is more
175 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and
176 Rijnsdorp, 2007b).

177

178 We change the parameters to implement different spatial structures for the
179 different populations using the *RandomFields* R package (Schlather et al., 2015).
180 We define a stationary habitat field with an anisotropic pattern (to simulate a
181 depth gradient) and combine it with a temporally dynamic thermal tolerance
182 field to imitate two key drivers of population dynamics without modelling the
183 processes explicitly. Each population was initialised at a single location, and

subsequently moved across the entire space according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature tolerance and distance from current cell:

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

Where $d_{I,J}$ is the euclidean distance between cell I and cell J , λ is a given rate of decay, $Hab_{c,p}$ is the 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 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)..

2.4. Fleet dynamics

Fleet dynamics were broadly categorised into three components. *Fleet targeting* determined the fleet catch efficiency and preference towards a particular

210 population; *trip-level decisions* determined the initial location to be fished at
 211 the beginning of a trip; and *within-trip decisions* determined fishing locations
 212 within a trip. This results in an explore-exploit strategy for individual vessels
 213 to maximise their catch from an unknown resource distribution (Bailey et al.,
 214 2019). The decision to use an individual based model for fishing vessels was
 215 taken because fishers are heterogeneous in their location choice behaviour due
 216 to different objectives, risk preference and targeting preference (Van Putten
 217 et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics
 218 are emergent from individual dynamics rather than pre-defined group dynamics.

219 2.4.1. Fleet targeting

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

227 2.4.2. Decision about where to fish at the start of a trip

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

238 2.4.3. *Decision about where to fish within a trip*

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

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

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

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

relationship:

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

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

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

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

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

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

2.4.4. Local population depletion

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

2.5. Fisheries-independent survey

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

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

2.6. Software: R-package development

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

3. Model calibration

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

3.1. Population models

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

314 3.2. Fleet calibration

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

325

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

335

336 3.3. Survey settings

337 The survey simulation was set up with a fixed gridded station design with
338 100 stations fished each year, starting on day 92 and ending on day 112 (5
339 stations per day) with same catchability parameter ($Q_p = 1$) for all populations.
340 This approximates a real world survey design with limited seasonal and spatial
341 coverage.

3.4. Example research question

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

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

To answer this question we compare different spatial and temporal aggregations of the true population distributions to:

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

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

The following steps are undertaken to determine closures:

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

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

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

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

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

387 4. Results

388 4.1. Emergent simulation dynamics

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

392 It can be seen from a single vessels movements during a trip that the ves-
393 sel exploits three different fishing grounds, each of them multiple times (Figure
394 2A), while across several trips fishing grounds that are further apart are fished

395 (Figure 2B). These different locations relate to areas where the highest revenue
396 were experienced, as shown by Figure 2D, where several vessels tracks are over-
397 laid on the revenue field.

398

399 Vessels from the same fleet (and therefore targeting preference) may exploit
400 some shared and some different fishing grounds depending on their own personal
401 experience during the exploratory phase of the fishery (Figure 2 (C)). This
402 results from the randomness in the correlated random walk step function, with
403 distance moved during the exploitation phase and the direction stochastically
404 related to the revenue experienced on the fishing ground (Figure 2 (D)).

405 *4.2. How does sampling-derived fisheries data reflect the underlying population*
406 *structure?*

407 Catch composition aggregated at different spatial resolutions from each of
408 the data sources (average seasonal patterns over a ten-year period) highlights dif-
409 ferent patterns in perceived community structure depending on the data source
410 and aggregation level (Figure 3). The finer spatial grid for the true popula-
411 tion (top left) and commercial data (top middle) show visually similar patterns,
412 though there are large unsampled areas in the commercial data from a lack
413 of fishing activity (particularly in the lower left part of the sampling domain).
414 Survey data at this spatial resolution displays very sparse information about
415 the spatial distributions of the populations. The slightly aggregated data on a
416 5 x 5 grid shows similar patterns and, while losing some of the spatial detail,
417 there remains good consistency between the true population and the commercial
418 data. Survey data starts to pick out some of the similar patterns as the other
419 data sources, but lacks spatiotemporal coverage. The spatial catch information
420 on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the
421 spatial resolutions for all data sources, and some differences between the survey,
422 commercial and true population data emerge.

423

424 Different perceptions of the proportion of each stock in an area are seen when

we aggregate the data at different timescales, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area showing different patterns (Figure 4). In the true population, the monthly aggregation captures the major patterns of composition seen in the weekly data with the percentage of different populations in the catch having similar mean and standard deviations (Table 7). In the weekly and monthly data population 2 dominates. However, some of the variation was lost when aggregated to an annual level, as indicated from the lower standard deviations (Table 7).

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

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

In most cases the fishery closure was successful in reducing fishing mortality on the species of interest (population 3; Figure 5). Interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries “adapted” to the closures by finding new areas of high abundance to fish. This led to fishing mortality increasing again, though not to past levels (Figure 5). The exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective (i.e. failed to reduce fishing mortality) with all data sources. As expected, closures based on the “known” population distribution were most effective, with differing degrees of success using the commercial data. Fishing mortality rates on the other species changed in different proportions, depending on whether the displaced fishing effort moved to areas where the populations

455 were found in greater or lesser density.

456

457 The factor most contributing to differences in fishing mortality before and
458 after the closure was the population (72 % showing that the closures were effective for population 3), followed by spatial data resolution (21 %), data type (7 %)
459 with the least important factor the timescale (< 1 %). In general the finer
460 the spatial resolution of the data used the greater reduction in fishing mortality
461 for population 3 after the closures (Figure 6). The notable outliers are the commercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
462 timescale, where closures were nearly as effective as the fine-scale resolution. In
463 this case the closures were sufficiently large to protect a core area of the habitat
464 for the population, but this was achieved in a fairly crude manner by closing a
465 large area - including area where the species was not found (Figure 7) that may
466 have consequences in terms of restricting the fishery in a much larger area than
467 necessary. We found that these trade-offs existed, with high catches maintained
468 with an effective closure when the highest resolution data was used, with the
469 effect being linear when the true population distribution was known and also
470 persisting for closures based on commercial information (Figure 8).

473

474 5. Discussion

475 Our study presents a new highly resolved fisheries simulation framework to
476 evaluate the importance of data scaling and considers potential bias introduced
477 through data aggregation when using fisheries data to infer spatiotemporal dynamics of fish populations. Understanding how fishers exploit multiple hetero-
478 geneously distributed fish populations with different catch limits or conservation
479 status requires detailed understanding of the overlap of resources; this is difficult
480 to achieve using conventional modelling approaches due to species targeting in
481 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
482 ten data are aggregated or extrapolated which requires assumptions about the

484 spatial and temporal scale of processes. Our study explores the assumptions
485 behind such aggregation and preferential sampling to identify potential impacts
486 on management advice. With modern management approaches increasingly
487 employing more nuanced spatiotemporal approaches to maximise productivity
488 while taking account of both the biological and human processes operating on
489 different time-frames (Dunn et al., 2016), understanding assumptions behind
490 the data used - increasingly a combination of logbook and positional informa-
491 tion from vessel monitoring systems - is vital to ensure measures are effective.

493 5.1. *Simulation dynamics*

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

499
500 Our approach is unique in that it captures fine scale population and fish-
501 ery dynamics and their interaction in a way not usually possible with real data
502 and thus not usually considered in fisheries simulations. While other simulation
503 frameworks seek to model individual vessel dynamics based on inferred dynam-
504 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
505 identify measures to meet particular management goals (Bailey et al., 2019),
506 our framework allows users to explore assumptions in modelling observational
507 data and to evaluate the underlying dynamics of such approaches at fine spatial
508 and temporal scales. This offers the advantage that larger scale fishery patterns
509 are emergent properties of the system and results can be compared to those
510 obtained under a statistical modelling framework.

511
512 Typically, simulation models that treat fish as individuals are focussed on
513 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 stochasticity, while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way.

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

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

541 *5.2. How does sampling-derived fisheries data reflect the underlying population*
542 *structure?*

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

550
551 Our simulation shows that, despite biases introduced through the fishing
552 process, the commercially derived data could still inform on the key spatial
553 patterns in the community structures where the fisheries occurred, which was
554 spatially limited due to the “hotspots” of commercially valuable species being
555 fished. Similarly, despite even spatial coverage the survey captured some of the
556 same spatial patterns as the true population, but missed others due to gaps be-
557 tween survey stations limiting spatial and temporal coverage (Figure 3). This
558 provides a challenge when modelling unsampled areas in inferring species distri-
559 bution maps, though these limitations may be overcome by understanding the
560 relationship between the species and habitat covariates where these are known
561 at unsampled locations (Robinson et al., 2011).

562
563 *5.3. How does data aggregation and source impact on spatial fisheries manage-*
564 *ment measures?*

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

569

570 The yearly data assumes the same proportion of each population caught
 571 at any time of the year due to the data aggregation. This assumption intro-
 572 duces ‘aggregation bias’ as the data may only be representative of some point
 573 (or no point) in time. The monthly data shows some consistency between the
 574 real population and commercial data for population 2 - 4, though population
 575 1 remains under-represented. On an annual basis, interestingly the commercial
 576 data under represents the first species while the survey over represents species
 577 1. This is likely due to the biases in commercial sampling, with the fisheries
 578 not targeting the areas where population 1 are present and the survey sampling
 579 areas where population 1 is more abundant than on average. This indicates that
 580 fixed closures, at the right resolution, when based on commercially derived data
 581 have the potential to reduce fishing mortality. The likely cost of poor spatial
 582 and temporal resolution is associated with reduced effectiveness and potentially
 583 closing fishing opportunities for other fisheries (Figure 8).

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

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

600 5.4. Model assumptions and caveats

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

605
606 Fish populations in our simulations move in pre-defined timescales and ac-
607 cording to fixed habitat preferences and temperature gradients (Figures S7, S9).
608 Our assumptions in calibrating the model (movement rates, temperature toler-
609 ances) will have a direct impact on our conclusions on the relative importance
610 of spatial and temporal processes. These assumptions could be explored in a
611 future study by varying the parameters and assessing the robustness of our con-
612 clusions. For our example application we have chosen movement rates to reflect
613 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

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

624 5.5. Future applications of *MixFishSim*

625 We consider that the increased availability of high resolution catch and lo-
626 cational information from commercial fisheries will make it a key source of data
627 for ensuring management is implemented at the right scale in future. For exam-
628 ple, identifying hot-spots for bycatch reduction or identifying spatial overlaps
629 in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al., 2015;

630 Dedman et al., 2015; Ward et al., 2015). Our simulation model has the potential
631 to test some of the assumptions behind the modelling approaches in identify-
632 ing such hotspots and indeed behind spatiotemporal modelling in general, e.g.
633 comparing GAMs, GLMMs, Random Forests and geostatistical models under
634 different data generation processes as exemplified by Stock et al. (2019).

635

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

650

651 6. Conclusions

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

659 and identity where data collection is needed to strengthen inference.

660

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

672

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

678

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684 competing interests.

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	Ford'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	€
$RefRev$	Reference revenue for determining the step function	€
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					
β_1	1	2	1	2	3
β_2	10	15	8	12	7
β_3 , the landings value nth 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)

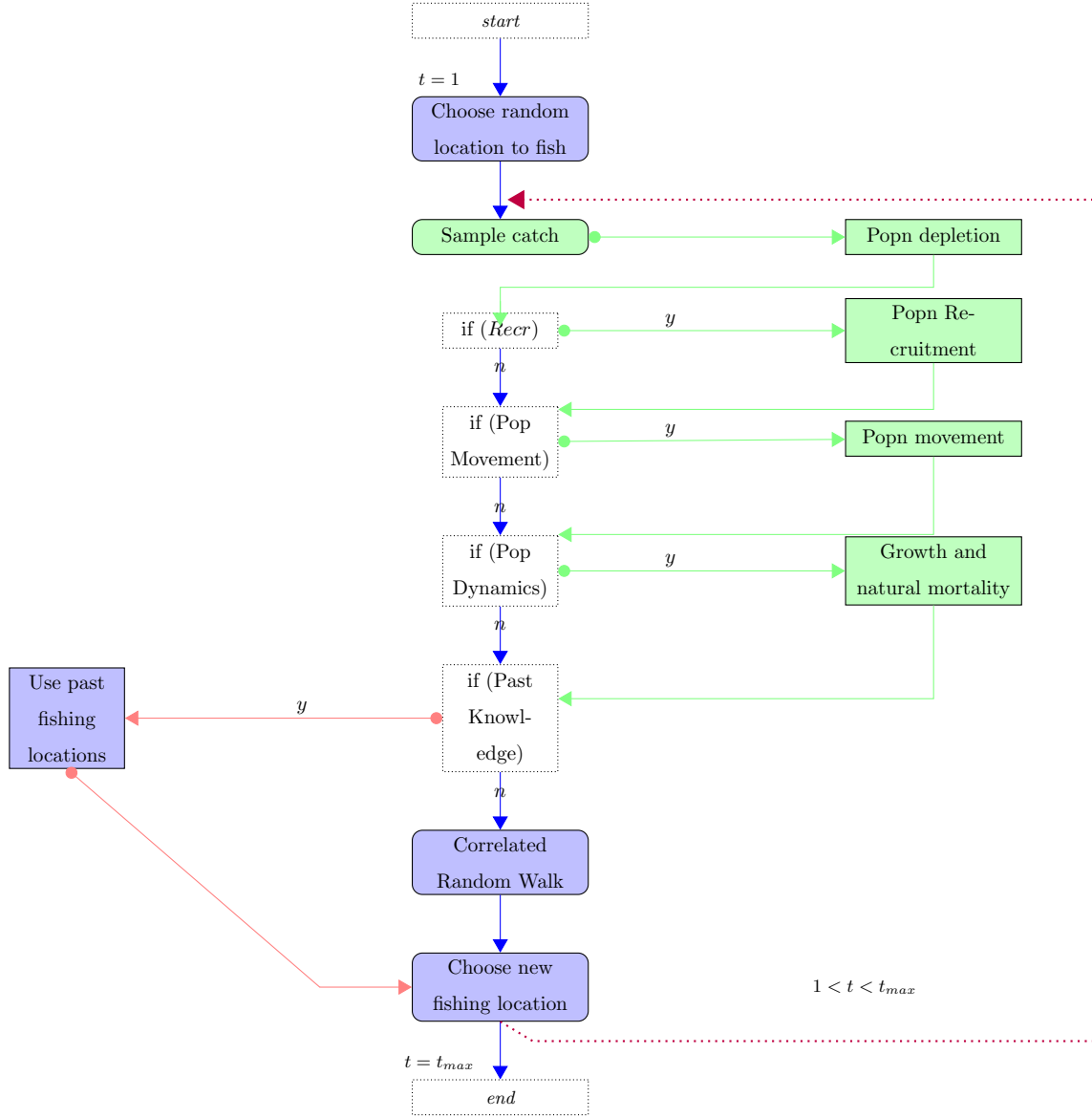


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Recr), (Pop Movement), (Pop Dynamics)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

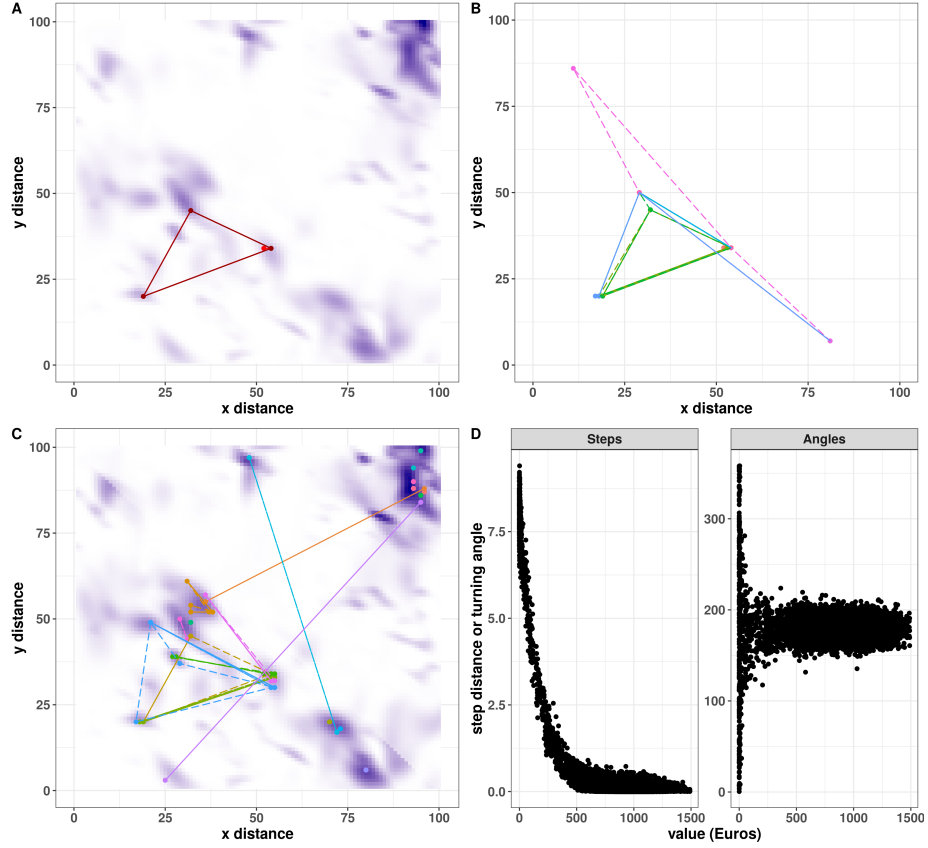


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not 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.

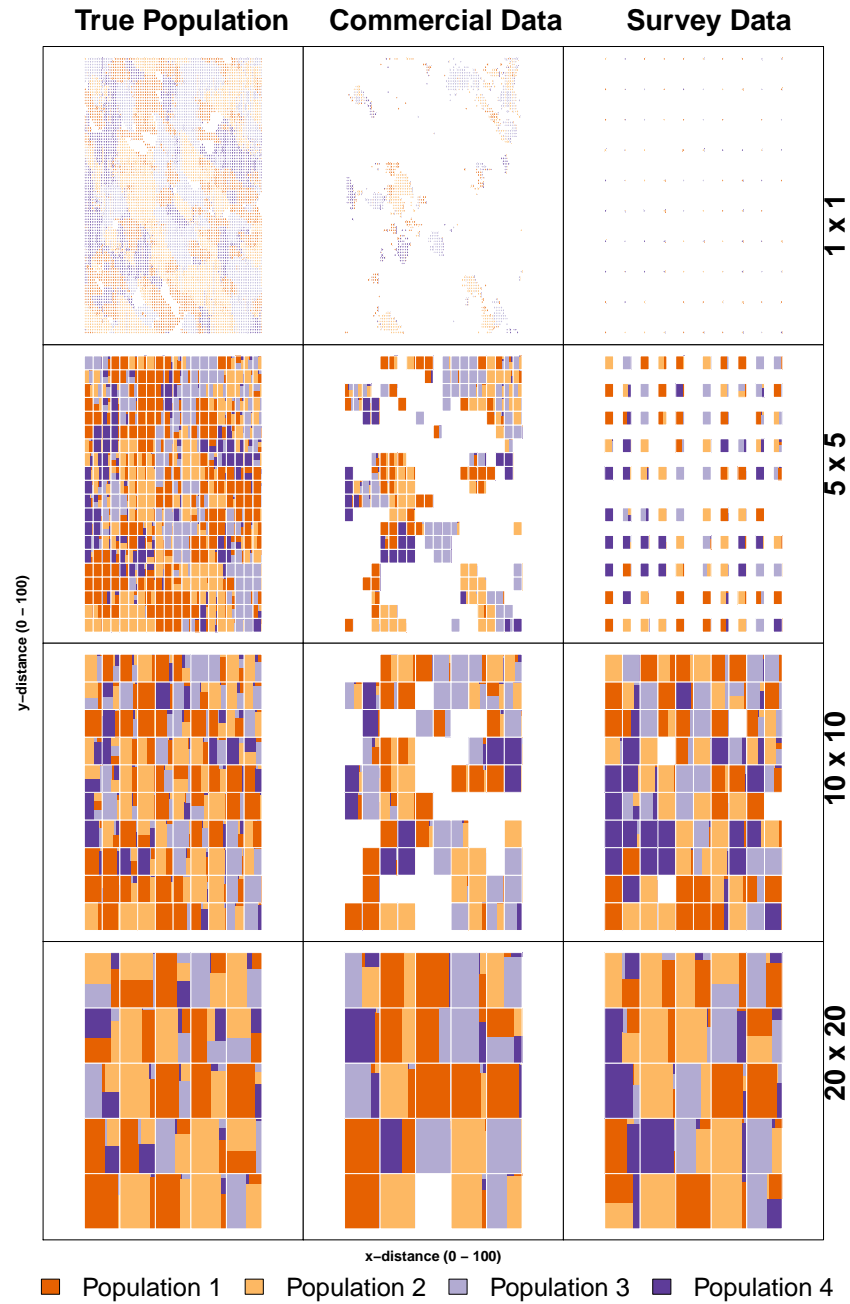


Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit.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

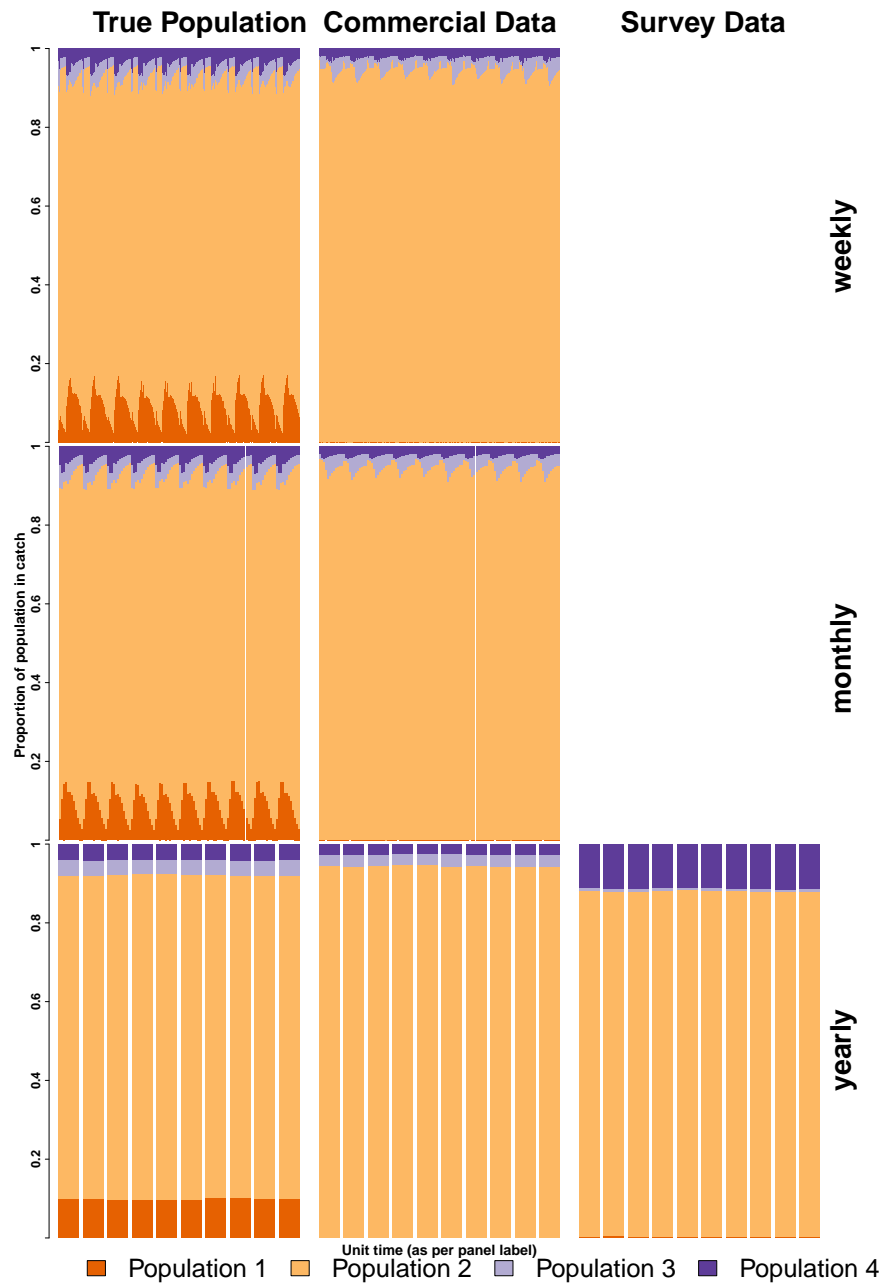


Figure 4: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

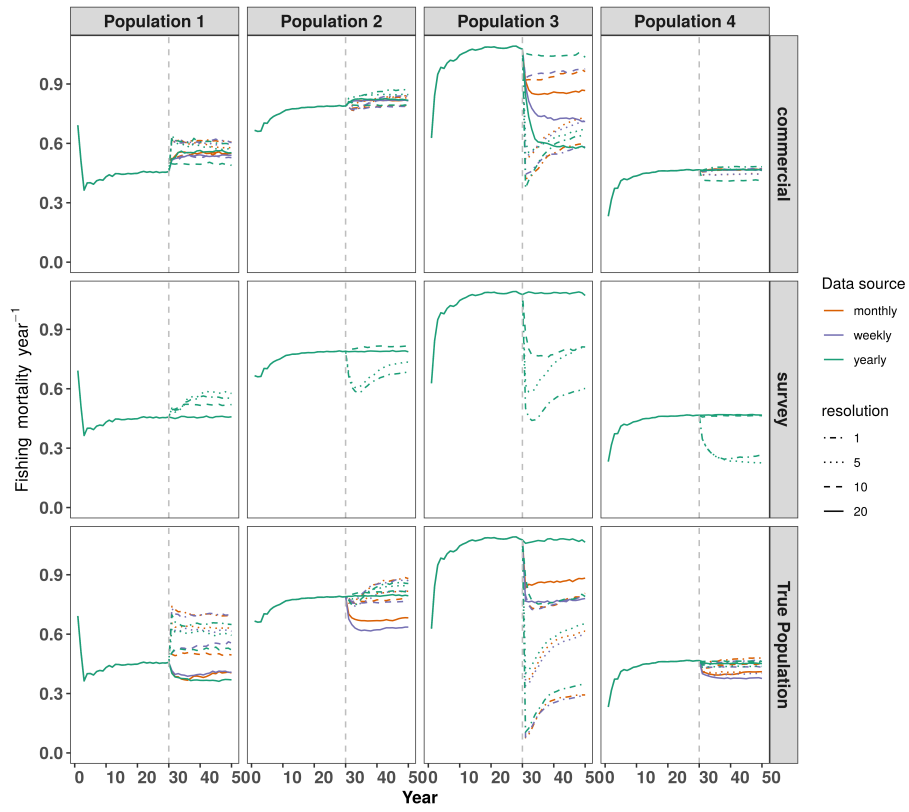


Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

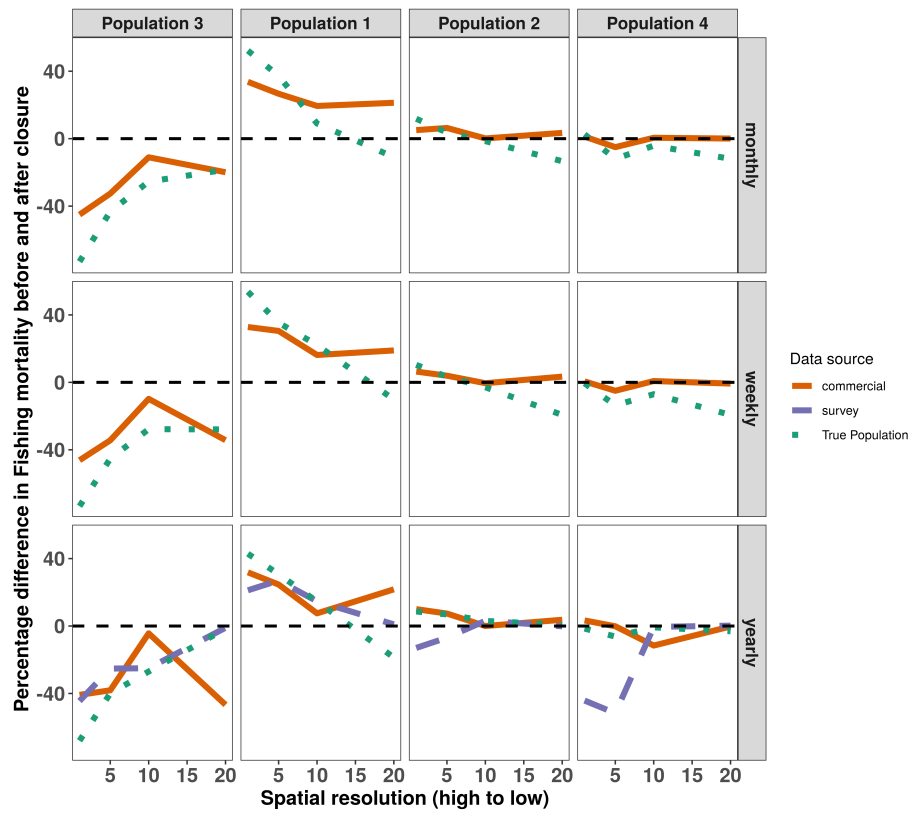


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

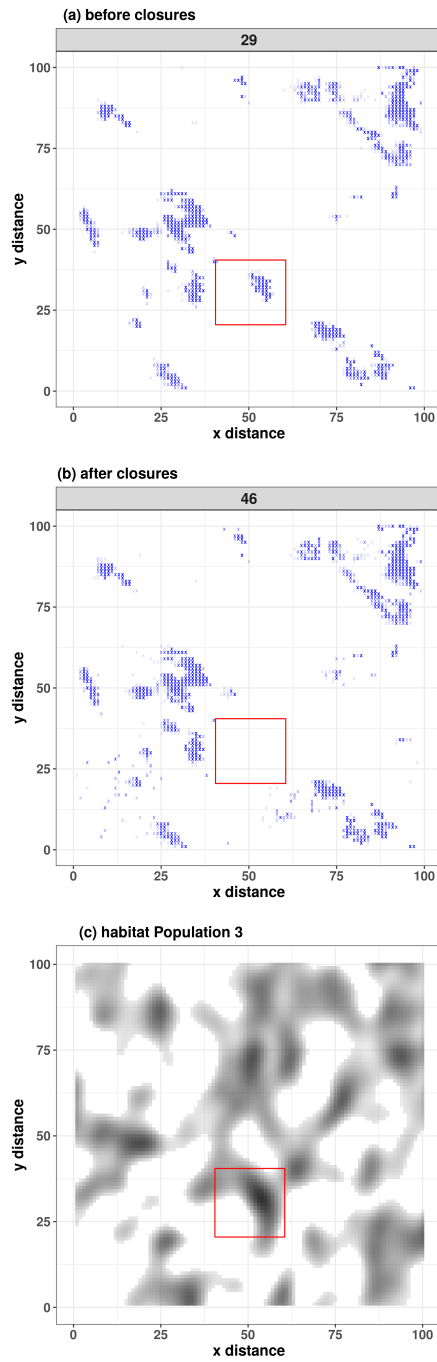


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

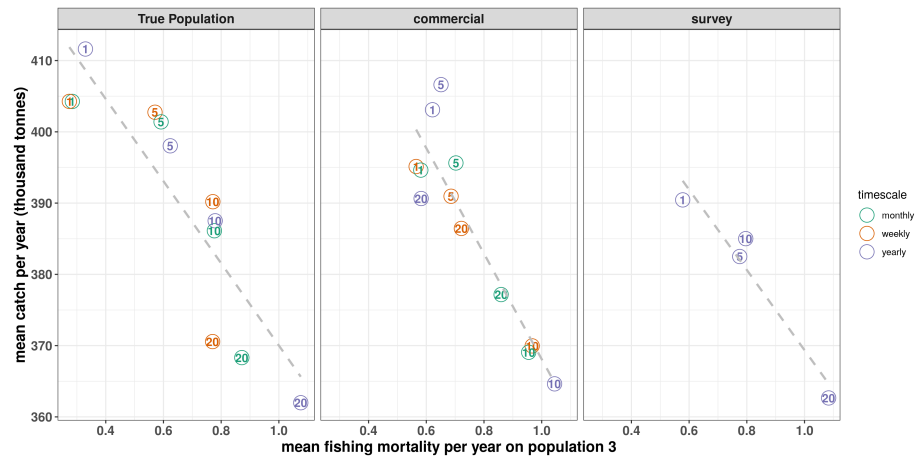


Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the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

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