

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 the framework to draw inference on community structure when using data generated from : commercial catch, a simulated fixed-site sampling survey design and the true (simulated) underlying populations. In doing so we establish the potential limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions We found different spatial patterns were evident and that the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. We then simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions. Aggregation across time periods has less of a negative impact on the closure success than over space. While not as effective as when

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

33

34

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

45

46 More refined spatiotemporal information has since become available through
47 the combination of logbook and Vessel Monitoring System (VMS) data (Lee
48 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2017)
49 and more real-time spatial management has been possible (e.g. Holmes et al.,

2011). However, fishers establish favoured fishing grounds through an explore-exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2019) where they search for areas with high catches and then use experience to return to areas where they’ve experienced high catch in the past. This leads to an inherently biased sampling where target species are over-represented in the catch as fishers exploit areas of high abundance. There is a need to understand the influence of these biases on any spatial management measures which are implemented based on inference from commercial landings or catch data.

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

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

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

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

82 **2. Materials and Methods**

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

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

97 *2.1. Population dynamics*

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

list is detailed in Table 1):

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

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

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

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

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, $C_{c,d} = \sum_{fl=1}^{FL} \sum_{v=1}^V E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$ with fl and FL the fleet and total number of fleets, v and V the vessel and total number of vessels 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 relationship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt

relationship is defined as (Beverton and Holt, 1957):

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

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:

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

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

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 which 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. The decision to model population movement on a weekly timescale was to reflect that fish tend to aggregate in species specific locations that have been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (Figure S7).

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

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

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

179

180 During pre-defined weeks of the year the habitat suitability is modified with

181 user-defined spawning habitat locations, resulting in each population having
 182 concentrated areas where spawning takes place. The populations then move to-
 183 wards these cells in the weeks prior to spawning, resulting in directional move-
 184 ment towards the spawning grounds.

185

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

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

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

194

195 2.4. Fleet dynamics

196 Fleet dynamics werebroadly categorised into three components. *Fleet tar-*
 197 *geting* determined the fleet catch efficiency and preference towards a particular
 198 population; *trip-level decisions* determined the initial location to be fished at
 199 the beginning of a trip; and *within-trip decisions* determined fishing locations
 200 within a trip. This results in an explore-exploit strategy for individual vessels
 201 to maximise their catch from an unknown resource distribution (Bailey et al.,
 202 2019). The decision to use an individual based model for fishing vessels was
 203 taken because fishers are heterogeneous in their location choice behaviour due
 204 to different objectives, risk preference and targeting preference (Van Putten
 205 et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics
 206 are emergent from individual dynamics rather than pre-defined group dynamics.

207 2.4.1. Fleet targeting

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

215 2.4.2. Decision about where to fish at the start of a trip

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

226 2.4.3. Decision about where to fish within a trip

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

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

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

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

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

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

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:

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

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

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

285 site (www.github.com/pdolder/MixFishSim).

286

287 **3. Model calibration**

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

290 *3.1. Population models*

291 We calibrated the simulation model for four example populations with dif-
292 ferent demographics, growth rates, natural mortality and recruitment (Table 4).
293 Habitat preference (Figure S3) and temperature (Figures S5, with temperature
294 tolerance S6) defined to be unique to each population resulting in differently
295 weekly distribution patterns (Figures S7-S9). In addition, each of the pop-
296 ulations was assumed to have two defined spawning areas that result in the
297 populations moving towards these areas in pre-defined weeks (Figure S4) with
298 population-specific movement rates (Table 4). The population demographics
299 were defined to broadly represent three mobile low-medium value groundfish
300 species and one high value species with low mobility, with the dynamics hypo-
301 thetical but as you might expect to find in a typical demersal fishery.

302 *3.2. Fleet calibration*

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

312 year so far (as defined per fleet in Table 5).

313

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

323

324 3.3. Survey settings

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

330 3.4. Example research question

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

338

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

341

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

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

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

353

354 The following steps are undertaken to determine closures:

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

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

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

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 S1) and consequently different sea-
 380 sonal exploitation patterns (Figure S2).

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

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

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

387 *4.2. How does sampling-derived fisheries data reflect the underlying population*
388 *structure?*

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

405
406 Different perceptions of the proportion of each stock in an area are seen when
407 we aggregate the data at different timescales, with weekly (top), monthly (mid-
408 dle) and yearly (bottom) catch compositions from across an aggregated 20 x 20
409 area showing different patterns (Figure 4). In the true population, the monthly
410 aggregation captures the major patterns of composition seen in the weekly data
411 with the percentage of different populations in the catch having similar mean
412 and standard deviations (Table 7). In the weekly and monthly data population
413 2 dominates. However, some of the variation was lost when aggregated to an
414 annual level, as indicated from the lower standard deviations (Table 7).

415
416 The commercial data on a weekly basis shows some of the same patterns as
417 the true population, though the population 1 is less well represented and some

418 weeks are missing catches from the area. Here, weekly and monthly composi-
419 tions were nearly identical (Figure 4; Table 7). Yearly values head a similar
420 mean but smaller standard deviation.

421

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

425 *4.3. How does data aggregation and source impact on spatial fisheries manage-*
426 *ment measures?*

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

440

441 The factor most contributing to differences in fishing mortality before and
442 after the closure was the population (72 % showing that the closures were ef-
443 fective for population 3), followed by data resolution (21 %), data type (7 %)
444 with the least important factor the timescale (< 1 %). In general the finer the
445 spatial resolution of the data used the greater reduction in fishing mortality for
446 population 3 after the closures (Figure 6). The notable outliers are the com-
447 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly

timescale, where closures were nearly as effective as the fine-scale resolution. In this case the closures were sufficiently large to protect a core area of the habitat for the population, but this was achieved in a fairly crude manner by closing a large area - including area where the species was not found (Figure 7) that may have consequences in terms of restricting the fishery in a much larger area than necessary. We found that these trade-offs existed, with high catches maintained with an effective closure when the highest resolution data was used, with the effect being linear when the true population distribution was known and also persisting for closures based on commercial information (Figure 8).

5. Discussion

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

477 5.1. *Simulation dynamics*

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

483
484 Our approach is unique in that it captures fine scale population and fish-
485 ery dynamics and their interaction in a way not usually possible with real data
486 and thus not usually considered in fisheries simulations. While other simulation
487 frameworks seek to model individual vessel dynamics based on inferred dynam-
488 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
489 identify measures to meet particular management goals (Bailey et al., 2019),
490 our framework allows users to explore assumptions in modelling observational
491 data and to evaluate the underlying dynamics of such approaches at fine spatial
492 and temporal scales. This offers the advantage that larger scale fishery patterns
493 are emergent properties of the system and results can be compared to those
494 obtained under a statistical modelling framework.

495
496 Typically, simulation models that treat fish as individuals are focussed on
497 exploring the inter- and intra- specific interactions among fish populations (e.g.
498 OSMOSE; Shin et al. (2004)) in order to understand how they vary over space
499 and time. Our focus was on understanding the strengths and limitations of
500 inference from catch data obtained through commercial fishing activity with
501 fleets exploiting multiple fish populations. This shows how realised catch distri-
502 butions may differ from the underlying populations, as identified by Gillis et al.
503 (2008). As such, we favoured a minimum realistic model of the fish populations
504 (Plagányi et al., 2014) taking account of environmental but not demographic
505 stochasticity, while incorporating detailed fishing dynamics that take account
506 of different drivers in a mechanistic way.

507

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).

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

Our results demonstrate the importance of considering data scale and resolution when using observational data to support management measures. We find that understanding of the community composition dynamics will depend on the level of data aggregation and its important to consider the scale of processes; including population movement rates, habitat uniformity and fishing targeting practices if potential biases in data are to be understood and taken into account (Figures S1, 2).

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

538 spatially limited due to the “hotspots” of commercially valuable species be-
 539 ing fished. Similarly, despite the even spatial coverage the survey was able to
 540 capture some of the same spatial patterns as the true population, but missed
 541 others due to gaps between survey stations limiting spatial and temporal cov-
 542 erage (Figure 3). This provides a challenge when modelling unsampled areas in
 543 inferring species distribution maps, though these limitations may be overcome
 544 by understanding the relationship between the species and habitat covariates
 545 where these are known at unsampled locations (Robinson et al., 2011).

547 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 548 *ment measures?*

549 From our simulations spatial disaggregation was more important than the
 550 temporal disaggregation of the commercial data. This reflects the fact that there
 551 was greater spatial heterogeneity over the spatial domain than experienced in
 552 individual locations over the course of the year (Figure S1).

553
 554 The yearly data assumes the same proportion of each population caught at
 555 any time of the year due to the data aggregation. This assumption introduces
 556 ‘aggregation bias’ as the data may only be representative of some point (or no
 557 point) in time. The monthly data shows some consistency between the real pop-
 558 ulation and commercial data for population 2 - 4, though population 1 remains
 559 under-represented. On an annual basis, interestingly the commercial data un-
 560 der represents the first species (in red) while the survey over represents species
 561 1. This is likely due to the biases in commercial sampling, with the fisheries
 562 not targeting the areas where population 1 are present and the survey sampling
 563 areas where population 1 is more abundant than on average. This indicates that
 564 fixed closures, at the right resolution, when based on commercially derived data
 565 have the potential to reduce fishing mortality. The likely cost of poor spatial
 566 and temporal resolution is associated with reduced effectiveness and potentially
 567 closing fishing opportunities for other fisheries (Figure 8).

568

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

578

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

584 *5.4. Model assumptions and caveats*

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

589

590 Fish populations in our simulations move in pre-defined timescales and ac-
 591 cording to fixed habitat preferences and temperature gradients (Figures S3, S5).
 592 Our assumptions in calibrating the model (movement rates, temperature toler-
 593 ances) will have a direct impact on our conclusions on the relative importance
 594 of spatial and temporal processes. These assumptions could be explored in a
 595 future study by varying the parameters and assessing the robustness of our con-
 596 clusions. For our example application we have chosen movement rates to reflect
 597 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

598

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

607

608 5.5. Future applications of *MixFishSim*

609 We consider that the increased availability of high resolution catch and lo-
610 cational information from commercial fisheries will require it to be a key source
611 of data for ensuring management is implemented at the right scale in future.
612 For example, identifying hot-spots for bycatch reduction or identifying spatial
613 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
614 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
615 potential to test some of the assumptions behind the modelling approaches in
616 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
617 eral, e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
618 els under different data generation processes as exemplified by Stock et al. (2019).

619

620 Other novel applications of our framework could be: testing different sur-
621 vey designs given multiple species and data generating assumptions (Xu et al.,
622 2015); commercial index standardisation methods and approaches and under-
623 standing of appropriate scales and data aggregations and non-proportionality
624 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
625 exploring assumptions about the distribution of natural mortality and fishing
626 mortality throughout the year and importance of capturing in-year dynamics
627 in estimating stock status (Liu and Heino, 2014); at sea sampling scheme de-

signs 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 in our application that there was greater spatial heterogeneity than temporal heterogeneity and that when using aggregated data to define spatial closures coarser temporal resolution (months instead of weeks) could still achieve the same results in reducing exploitation rates of a vulnerable species at the highest temporal resolution data. Conversely, reducing the spatial resolution had a negative effect on the effectiveness of the measures (though importantly, there was still some benefit even with coarse spatial resolution).

657

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

663

664 *MixFishSim* has numerous potential additional applications as it enables
665 the user to apply methods to a fisheries system where there is detailed under-
666 standing of underlying spatiotemporal dynamics. This enables identification of
667 weaknesses or limitations which would not be possible otherwise. In future, we
668 recommend use of the framework to test hypotheses that are otherwise unable
669 to be analysed using real world data due to limitations of data collection. That
670 way the knowledge gained through simulation can inform the future design of
671 management measures.

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677 competing interests.

678 **Appendices**

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

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

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

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

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

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

Table 4: Population dynamics and movement parameter settings.

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

Table 5: Fleet dynamics parameter setting.

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

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

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

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

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

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

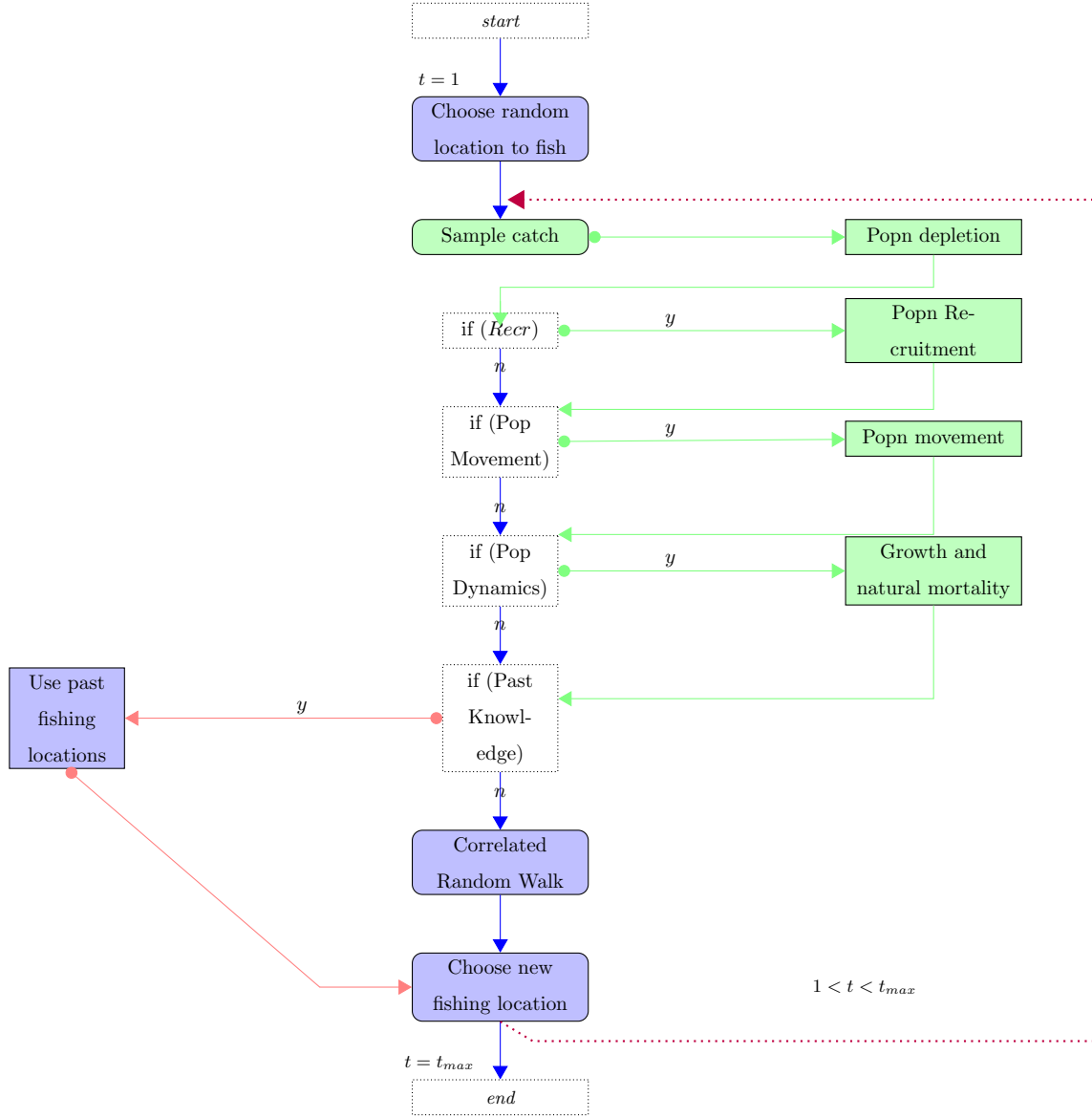


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Recr), (Pop Movement), (Pop Dynamics)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

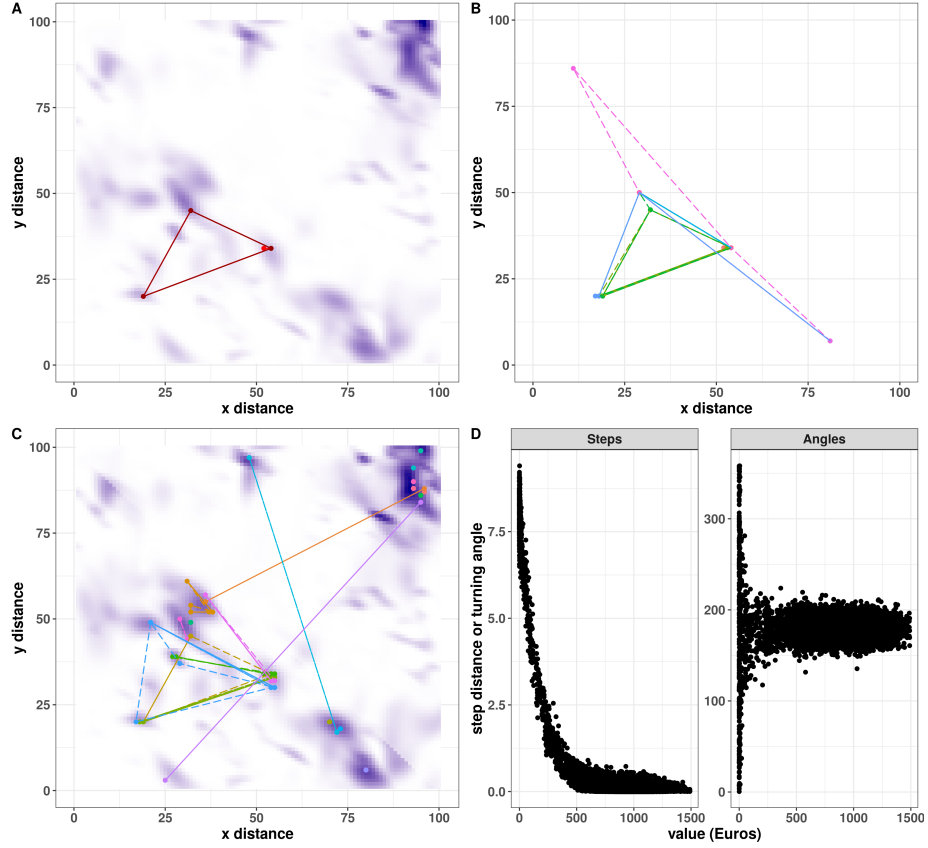


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not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

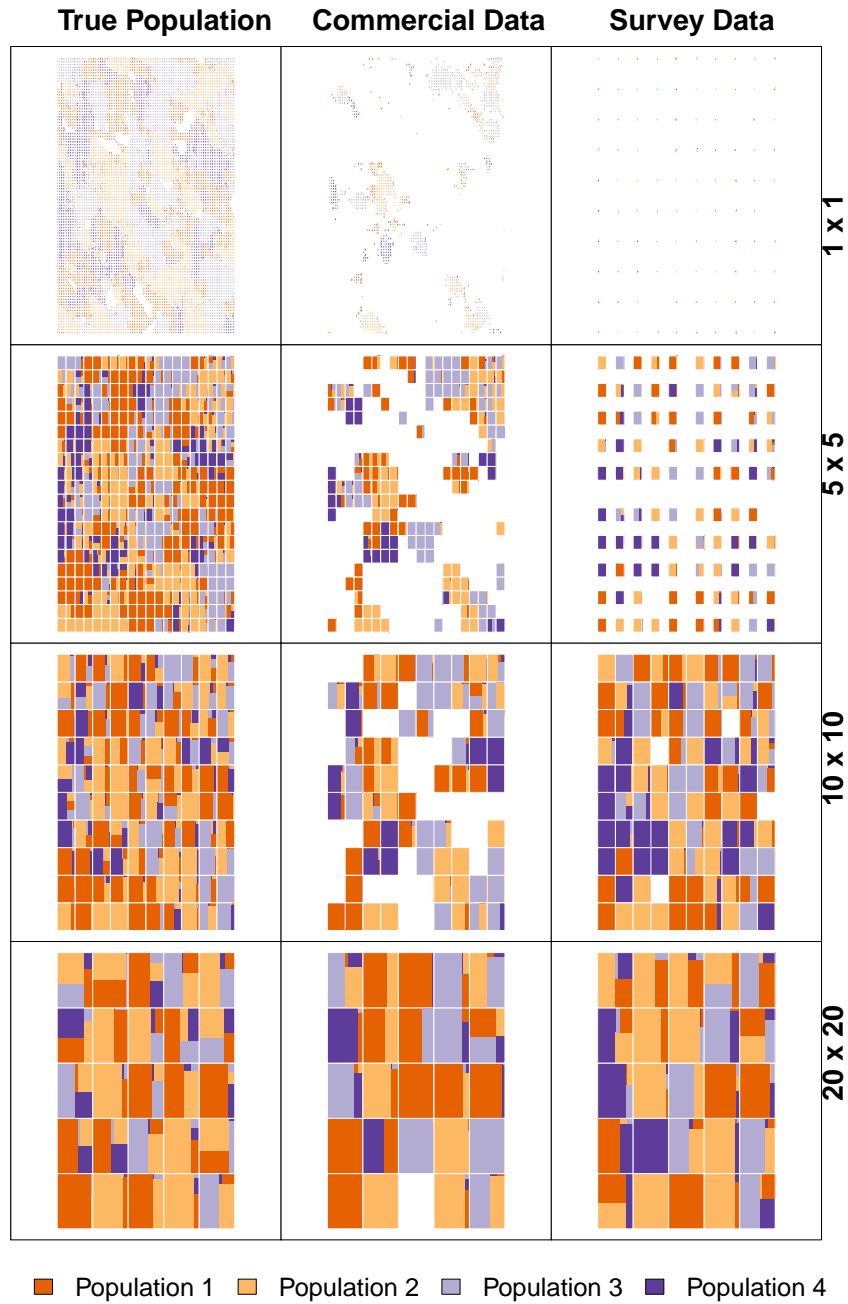


Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit.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

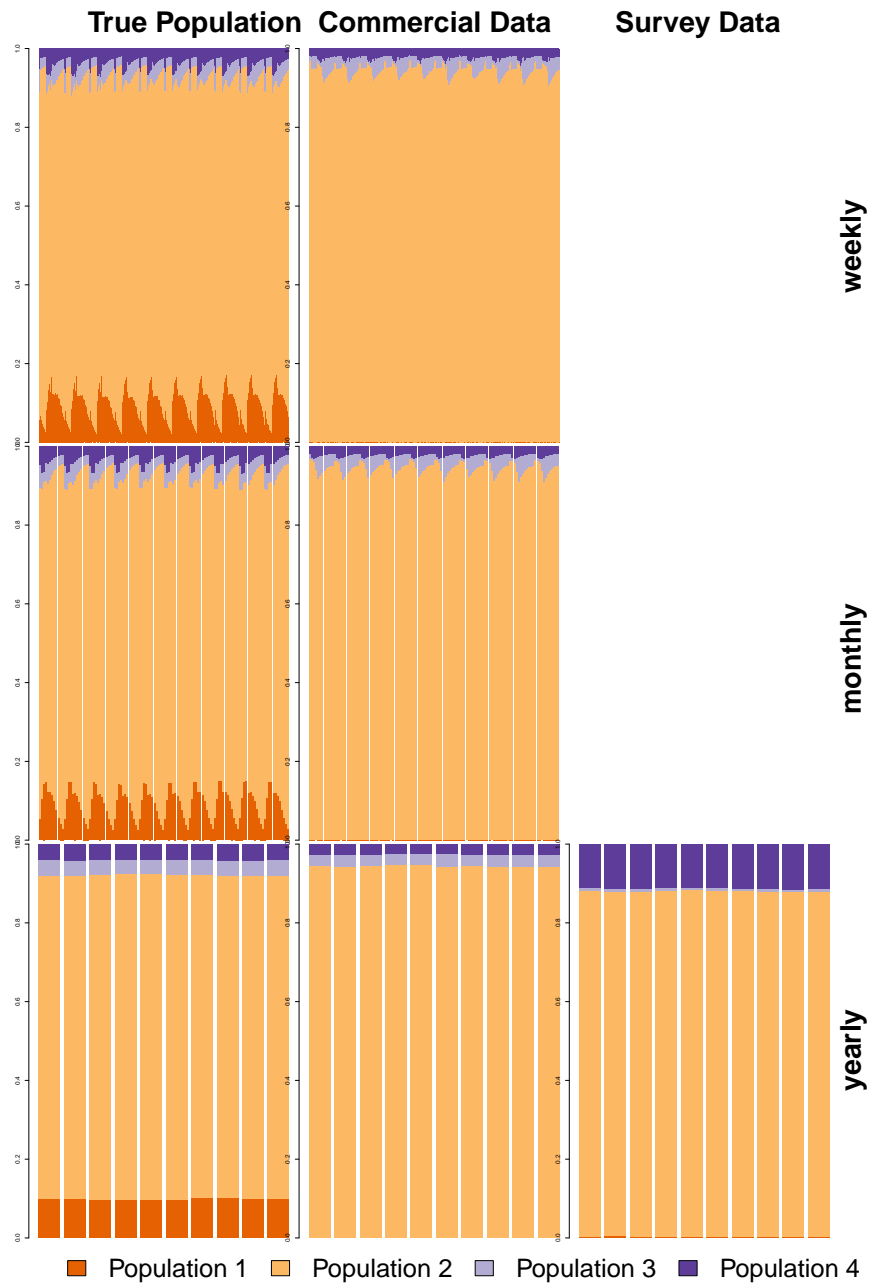


Figure 4: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

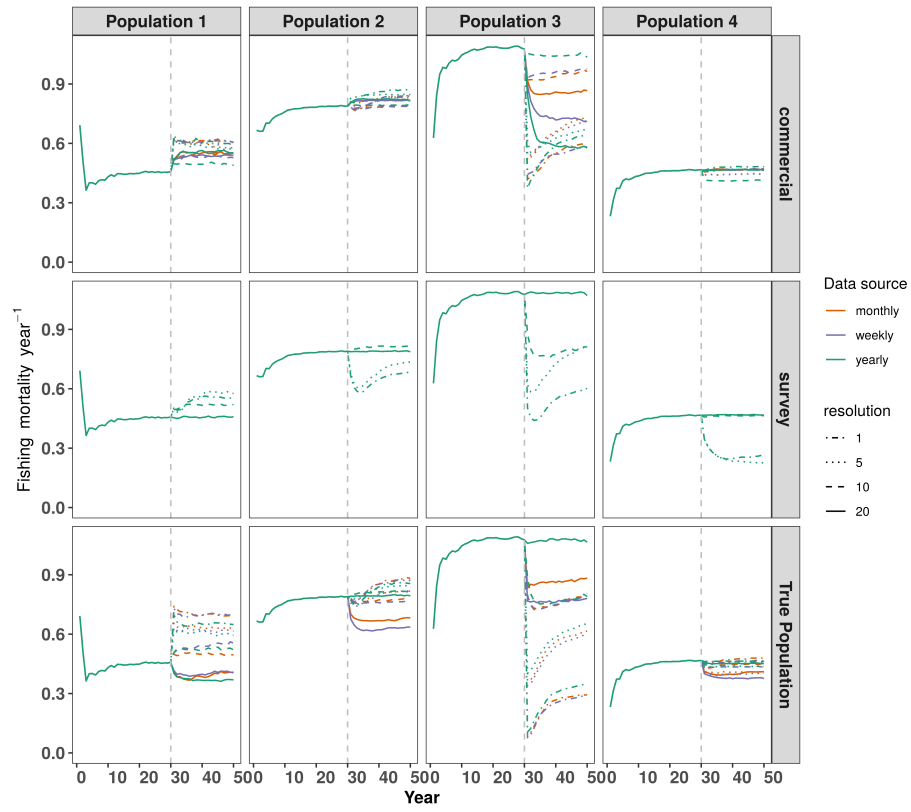


Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

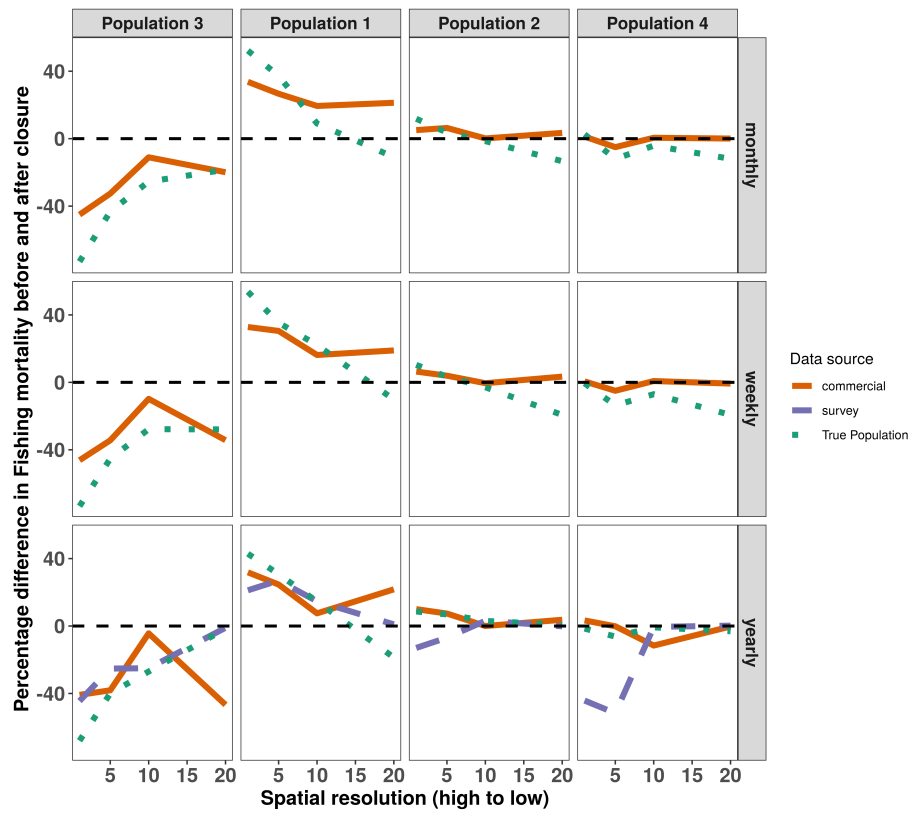


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

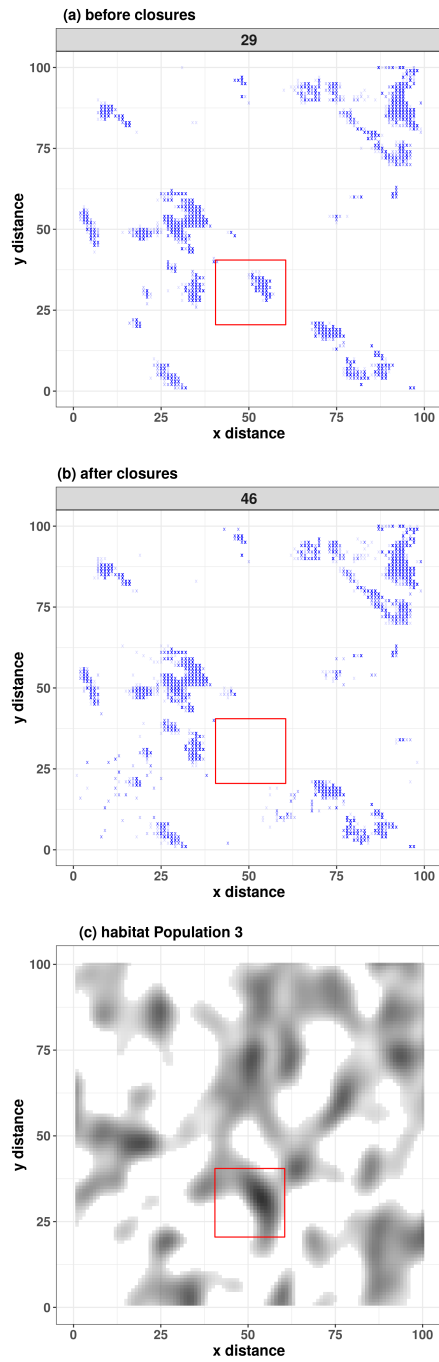


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

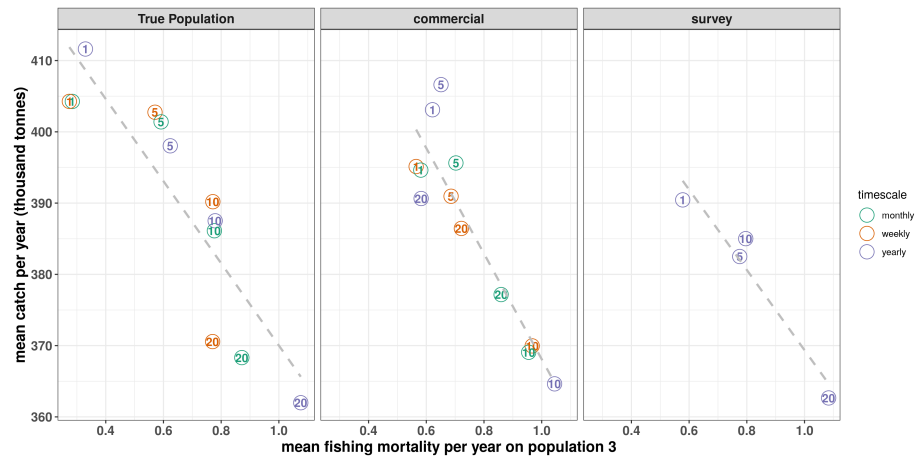


Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the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

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