

Working title: Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder^{a,b,*}, C  il  n Minto^a, Jean-Marc Guarini^c, Jan Jaap Poos^{d,e}

^a*Galway-Mayo Institute of Technology (GMIT), Dublin Road, Galway, Ireland*

^b*Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, UK*

^c*Sorbonne Universit  , Faculty of Sciences, 4 Place Jussieu, 75005 Paris, France*

^d*Wageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands*

^e*Aquaculture and Fisheries Group, Wageningen University & Research, Zodiac Building 122, De Elst 1, 6708 WD Wageningen, the Netherlands*

Abstract

To understand how data resolution impacts inference on mixed fisheries interactions we developed a highly resolved spatiotemporal discrete-event simulation model incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on population targeting under an explore-exploit strategy. This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

Fifty years of sub-daily fishing activity was simulated and used to draw inference on the underlying community structures. We compared inferences based on: commercial catch, a simulated fixed-site sampling survey design and the true underlying populations. We i) establish the potential limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and then ii) simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions.

Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine

*Corresponding author

Email address: paul.dolder@gmit.ie (Paul J. Dolder)

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

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

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1. Introduction

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

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019) and adaptive spatial management strategies have been proposed as a way of reduc-

16 ing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al.,
17 2014). However, if fisheries are to reduce unwanted catch through spatial avoid-
18 ance, an in-depth understanding of spatiotemporal fishery dynamics is required.

19
20 Understanding the correct scale for spatial management measures to be effec-
21 tive is crucial as it enables implementation of effective solutions which minimise
22 economic impact (Dunn et al., 2016). For example, the problem can be to iden-
23 tify a scale that promotes species avoidance for vulnerable or low quota species
24 while allowing continuance of sustainable fisheries for available quota species.
25 Identifying the correct spatial scale remains a challenge because data on fish
26 location at high temporal and spatial resolutions is expensive and difficult to
27 collect and proxies are usually inferred from scientific surveys or commercial
28 catches with limited spatial and temporal resolution. Thus, implementation of
29 spatial measures is hampered by a lack of knowledge of fish and fishery spa-
30 tiotemporal dynamics and understanding of the scale at which these processes
31 become important for management.

32
33
34 Identifying appropriate spatial scales for fisheries closures has been a high-
35 lighted as crucial to their success (Costello et al., 2010; Dunn et al., 2016).
36 Inference on fisheries spatial dynamics is hampered where spatial information
37 is coarse due to low resolution reporting of fisheries catch which is aggregated
38 across larger gridded areas (Branch et al., 2005). Further, if data does not allow
39 identification of spatial features it may lead to poorly sited closures which are
40 ineffectual or have unintended consequences. For example, increased benthic
41 impact on previously unexploited areas from the cod closure in the North Sea
42 were observed without the intended effect of reducing cod exploitation (Rijns-
43 dorp et al., 2001; Dinmore et al., 2003)).

44
45 More refined spatiotemporal information has since become available through
46 the combination of logbook and Vessel Monitoring System (VMS) data (Lee

et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). However, fishers establish favoured fishing grounds through an explore-exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2018) where they search for areas with high catches and then use experience to return to areas where they've experienced high catch in the past. This leads to an inherently biased sampling where target species are over-represented in the catch as fishers exploit 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 reflects 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.

76 We then iii) simulate a fishery closure to protect a species based on different
77 spatial and temporal data aggregations.

78

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

81 2. Materials and Methods

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

89

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

93 2.1. Population dynamics

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

To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the populations on a 2d grid. We first defined a Gaussian random field process, $\{S(c) : c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S = \{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure, where the correlation strength weakens with distance controlled by two parameters, with ν a scale parameter in the units of distance and κ a shape parameter which determines the smoothness of the process. This enables us to model the spatial autocorrelation observed in animal populations where density is more similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and

150 Rijnsdorp, 2007b) and we change the parameters to implement different spa-
 151 tial structures for the different populations using the *RandomFields* R package
 152 (Schlater et al., 2015). We define a stationary habitat field with an anisotropic
 153 pattern (to simulate a depth gradient) and combine it with a temporally dy-
 154 namic thermal tolerance field to imitate two key drivers of population dynamics
 155 without modelling the processes explicitly. Each population was initialised at a
 156 single location, and subsequently moved across the entire space according to a
 157 probabilistic distribution based on habitat suitability (represented by the nor-
 158 malised values from the GRFs), temperature and distance from current cell:

$$159 \quad Pr(C_{wk+1} = J | C_{wk} = I) = \frac{e^{-\lambda \cdot d_{I,J}} \cdot (Hab_{J,p}^2 \cdot Tol_{J,p,wk})}{\sum_{c=1}^C e^{-\lambda \cdot d} \cdot (Hab_{c,p}^2 \cdot Tol_{c,p,wk})} \quad (5)$$

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

164
 165 During pre-defined weeks of the year the habitat suitability is modified with
 166 user-defined spawning habitat locations, resulting in each population having
 167 concentrated areas where spawning takes place. The populations then move to-
 168 wards these cells in the weeks prior to spawning, resulting in directional move-
 169 ment towards the spawning grounds.

170
 171 A time-varying temperature covariate changes the interaction between time
 172 and suitable habitat on a weekly time-step. Each population p was assigned a
 173 thermal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and popula-
 174 tion temperature suitability is defined that:

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

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

177 deviation of the population temperature tolerance.

178

179 The final combined process results in a population structure and movement
180 pattern unique to each population, with population movement occurring on a
181 weekly basis. The decision to model population movement on a weekly timescale
182 was to reflect that fish tend to aggregate in species specific locations that have
183 been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).
184 Therefore this process approximated the demographic shifts in fish populations
185 throughout a year with seasonal spawning patterns (Figure S5).

186 2.4. Fleet dynamics

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

200 2.4.1. Fleet targeting

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

206 randomness from the exploratory fishing process) determined the preference of
207 fishing locations for the fleet.

208 *2.4.2. Decision about where to fish at the start of a trip*

209 Several studies (for a review see Girardin et al., 2016) have confirmed past
210 activity and past catch rates are strong predictors of fishing location choice.
211 For this reason, the fleet dynamics sub-model included a learning component,
212 where a vessel’s initial fishing location in a trip was based on selecting from
213 previously successful fishing locations. This was achieved by calculating an
214 expected revenue based on the catches from locations fished in the preceding
215 trip as well as the same month periods in previous years and the travel costs
216 from the port to the fishing grounds. Then a vessel chooses randomly from the
217 top 70 % of fishing events (defined as the ‘threshold’) in terms of expected profit
218 within that season.

219 *2.4.3. Decision about where to fish within a trip*

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

233

234 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:

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

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

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

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.

254 2.4.4. Local population depletion

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

264 2.5. Fisheries independent survey

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

272

273 2.6. Software: R-package development

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

277

278 3. Parameterisation

279 We parameterise *MixFishSim* to investigate the influence of data aggregation
280 on spatial inference.

281 3.1. Population models

282 We parametrised the simulation model for four example populations with
283 different demographics, growth rates, natural mortality and recruitment pa-
284 rameters (Table 4). Habitat preference (Figure S1) and temperature (Figures
285 S3, with temperature tolerance S4) defined to be unique to each population
286 resulting in differently weekly distribution patterns (Figures S5-S7). In addi-
287 tion, each of the populations was assumed to have two defined spawning areas
288 that result in the populations moving towards these areas in pre-defined weeks
289 (Figure S2) with population-specific movement rates (Table 4).

290 3.2. Fleet parametrisation

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

301
302 Fishing locations were chosen based on random search and, with increasing
303 proportion as time progressed, experience of profitable catches built up in the
304 same month from previous years and from the previous trip. 'Profitable' in
305 this context was defined as the locations where the top 70 % of expected profit
306 would be found given revenue from previous trips and cost of movement to the
307 new fishing location. This probability was based on a logistic sigmoid function
308 with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate
309 that ensures the upper asymptote (where decisions are mainly based on past

310 knowledge) is reached approximately halfway through the simulation.

311

312 3.3. Survey settings

313 The survey simulation was set up with a fixed gridded station design with
314 100 stations fished each year, starting on day 92 and ending on day 112 (5
315 stations per day) with same catchability parameter ($Q_p = 1$) for all populations
316 p . This approximates a real world survey design with limited seasonal and
317 spatial coverage.

318 3.4. Example research question

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

326

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

329

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

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

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

341

342 The following steps are undertaken to determine closures:

- 343 1. Extract data source (true population, commercial or survey),
- 344 2. Aggregate according to desired spatial and temporal resolution,
- 345 3. Interpolate across entire area at desired resolution using simple bivariate
346 interpolation using the *interp* function from the R package *akima* (Akima,
347 2006). This is intended to represent a naive spatial model of catch rates,
348 without knowledge of the spatial population dynamics.
- 349 4. Close area covering top 5 % of catch rates

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

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

355 Survey closures were on an annual basis only, as this was the most temporally
356 resolved survey data available. We evaluated the factors contributing to the
357 success of the closures through a regression tree (using the R package *REEMtree*
358 (Sela and Simonoff, 2012)) to identify the factor most contributing to differences
359 in fishing mortality before and after the closure.

360 4. Results

361 4.1. Emergent simulation dynamics

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

It can be seen from a single vessels movements during a trip that the ves-
sel exploits three different fishing grounds, each of them multiple times (Figure
4(A)), while across several trips fishing grounds that are further apart are fished
(Figure 4 (B)). These different locations relate to areas where the highest rev-
enue were experienced, as shown by Figure 4 (D), where several vessels tracks
are overlaid on the revenue field, i.e.

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

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

371 4.2. How does sampling-derived fisheries data reflect the underlying population 372 structure?

373 The aggregated catch composition from each of the data sources over a ten-
374 year period (which shows average seasonal patterns) at different spatial resolu-
375 tions highlights different patterns in perceived community structure depending
376 on the data source and aggregation level (Figure 5). The finer spatial grid for
377 the true population (top left) and commercial data (top middle) show visually
378 similar patterns, though there are large unsampled areas in the commercial data
379 from a lack of fishing activity (particularly in the lower left part of the sam-
380 pling domain). The survey data at this spatial resolution displays very sparse

information about the spatial distributions of the populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns and, while losing some of the spatial detail, there remains good consistency between the true population and the commercial data. Survey data starts to pick out some of the similar patterns as the other data sources, but lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the spatial resolutions for all data sources, and some differences between the survey, commercial and true population data emerge.

Different perceptions of the proportion of each stock in an area are seen when we aggregate the data over a smaller geographical region at different timescales, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area (Figure 6). 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. In the weekly data population 1 = 9.36% (SD = 3.99), population 2 = 83.2% (5.60), population 3 = 3.57% (1.23), population 4 = 3.91% (1.59); in the monthly data population 1 = 9.23% (3.87), population 2 = 83.3 (5.52), population 3 = 3.62% (1.15), population 4 = 3.86 (1.52). While means were similar some of the variation was lost when aggregated to an annual level; population 1 = 9.90% (0.173), population 2 = 82.2% (0.308), population 3 = 3.82% (0.119), population 4 = 4.03% (0.0502).

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

412 The survey data was only available on an annual basis, and showed again a
 413 slightly different composition; population 1 = 0.372% (0.00473), population 2 =
 414 87.7% (0.193), population 3 = 0.729% (0.0200), population 4 = 11.2% (0.172).

415 *4.3. How does data aggregation and source impact on spatial fisheries manage-* 416 *ment measures?*

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

422 In most cases the fishery closure was successful in reducing fishing mortal-
 423 ity on the species of interest (population 3; Figure 7), though interestingly the
 424 largest reductions in fishing mortality happened immediately after the closures,
 425 following which the fisheries “adapted” to the closures and fishing mortality
 426 increased again somewhat. The exception to the success was the closures imple-
 427 mented based on the coarsest spatial (20 x 20) and temporal resolution (yearly)
 428 that was ineffective (i.e. failed to reduce fishing mortality) with all data sources.
 429 As expected, closures based on the “known” population distribution were most
 430 effective, with differing degrees of success using the commercial data. Fishing
 431 mortality rates on the other species changed in different proportions, depending
 432 on whether the displaced fishing effort moved to areas where the populations
 433 were found in greater or lesser density.

434
 435 The factor most contributing to differences in fishing mortality before and
 436 after the closure was the population (72 % showing that the closures were ef-
 437 fective for population 3), followed by data resolution (21 %), data type (7 %)
 438 with the least important factor the timescale (< 1 %). In general the finer the
 439 spatial resolution of the data used the greater reduction in fishing mortality for
 440 population 3 after the closures (Figure 8). The notable outliers are the com-
 441 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 9) that may have consequences in terms of restricting the fishery in a much larger area than necessary. We found that these trade-offs existed, with high catches maintained with an effective closure when the highest resolution data was used, with the effect being linear when the true population distribution was known and also persisting for closures based on commercial information (Figure 10).

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.

471 5.1. *Simulation dynamics*

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

477
478 Our approach is unique in that it captures fine scale population and fish-
479 ery dynamics and their interaction in a way not usually possible with real data
480 and thus not usually considered in fisheries simulations. While other simulation
481 frameworks seek to model individual vessel dynamics based on inferred dynam-
482 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
483 identify measures to meet particular management goals (Bailey et al., 2018), our
484 framework allows users to explore the assumptions in modelling observational
485 data and evaluate the underlying dynamics of such approaches at a fine spatial
486 and temporal scale. This offers the advantage that larger scale fishery patterns
487 are emergent properties of the system and results can be compared to those
488 obtained under a statistical modelling framework.

489
490 Typically, simulation models that treat fish as individuals are focussed on
491 exploring the inter- and intra- specific interactions among fish populations (e.g.
492 OSMOSE; Shin et al. (2004)) in order to understand how they vary over space
493 and time. Our focus was on understanding the strengths and limitations of in-
494 ference from catch data obtained through commercial fishing activity with fleets
495 exploiting multiple fish populations and realising catch distributions that may
496 differ from the underlying populations, as identified by Gillis et al. (2008). As
497 such, we favoured a minimum realistic model of the fish populations (Plagányi
498 et al., 2014) taking account of environmental but not demographic stochastic-
499 ity, while incorporating detailed fishing dynamics that take account of different
500 drivers in a mechanistic way.

501

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., 2018).

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

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

Our simulation shows that, despite biases introduced through the fishing process, the commercially derived data could still inform on the key spatial patterns in the community structures where the fisheries occurred, which was

532 spatially limited due to the “hotspots” of commercially valuable species be-
533 ing fished. Similarly, despite the even spatial coverage the survey was able to
534 capture some of the same spatial patterns as the true population, but missed
535 others due to gaps between survey stations limiting spatial and temporal cov-
536 erage (Figure 5). This provides a challenge when modelling unsampled areas in
537 inferring species distribution maps, though these limitations may be overcome
538 by understanding the relationship between the species and habitat covariates
539 where these are known at unsampled locations (Robinson et al., 2011).

540

541 *5.3. How does data aggregation and source impact on spatial fisheries manage-*
542 *ment measures?*

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

547

548 The yearly data assumes the same proportion of each population caught at
549 any time of the year due to the data aggregation. This assumption introduces
550 ‘aggregation bias’ as the data may only be representative of some point (or no
551 point) in time. The monthly data shows some consistency between the real pop-
552 ulation and commercial data for population 2 - 4, though population 1 remains
553 under-represented. On an annual basis, interestingly the commercial data un-
554 der represents the first species (in red) while the survey over represents species
555 1. This is likely due to the biases in commercial sampling, with the fisheries
556 not targeting the areas where population 1 are present and the survey sampling
557 areas where population 1 is more abundant than on average. This indicates that
558 fixed closures, at the right resolution, when based on commercially derived data
559 have the potential to reduced fishing mortality. The likely cost of poor spatial
560 and temporal resolution is associated with reduced effectiveness and potentially
561 closing fishing opportunities for other fisheries (Figure 10).

562

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

572

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

578 *5.4. Model assumptions and caveats*

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

583

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

592

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

601

602 5.5. Future applications of *MixFishSim*

603 We consider that the increased availability of high resolution catch and lo-
 604 cational information from commercial fisheries will require it to be a key source
 605 of data for ensuring management is implemented at the right scale in future.
 606 For example, identifying hot-spots for bycatch reduction or identifying spatial
 607 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
 608 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
 609 potential to test some of the assumptions behind the modelling approaches in
 610 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
 611 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
 612 els under different data generation processes as exemplified by Stock et al. (2019)).

613

614 Other novel applications of our framework could be: testing different sur-
 615 vey designs given multiple species and data generating assumptions (Xu et al.,
 616 2015); commercial index standardisation methods and approaches and under-
 617 standing of appropriate scales and data aggregations and non-proportionality
 618 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
 619 exploring assumptions about the distribution of natural mortality and fishing
 620 mortality throughout the year and importance of capturing in-year dynamics
 621 in estimating stock status (Liu and Heino, 2013); 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., 2016); and as a detailed operating model in a management strategy evaluation (Mahévas and Pelletier, 2004).

6. Conclusions

MixFishSim provides a detailed simulation framework to explore the interaction of multiple fisheries exploiting different fish populations. The framework enables users to evaluate assumptions in modelling commercially derived data through comparison to the true underlying dynamics at a fine spatial and temporal scale. Understanding these dynamics, the limitations of the data and any 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).

651

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

657

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

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670 **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^2	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; (Rec), (Pop Movement), (Pop Dynamics) logic gates for recruitment periods, population movement and population dynamics for each of the populations, (Past Knowledge) a switch whether to use a random (exploratory) or past knowledge (exploitation) fishing strategy.

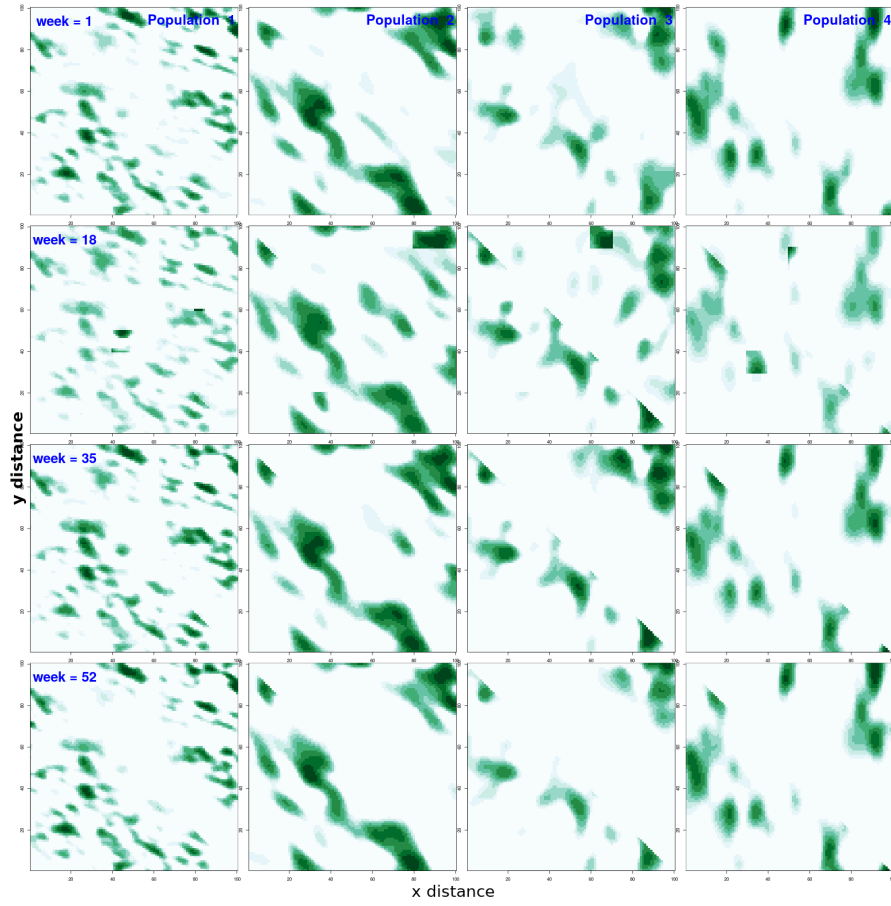


Figure 2: Spatial density (log abundance) for each of the four populations at four time steps. The darker the colour the greater the density of the population. Note that a diagonal anisotropic pattern (mimicking a depth gradient) can be clearly seen in populations 2 and 3. The concentrated spawning areas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

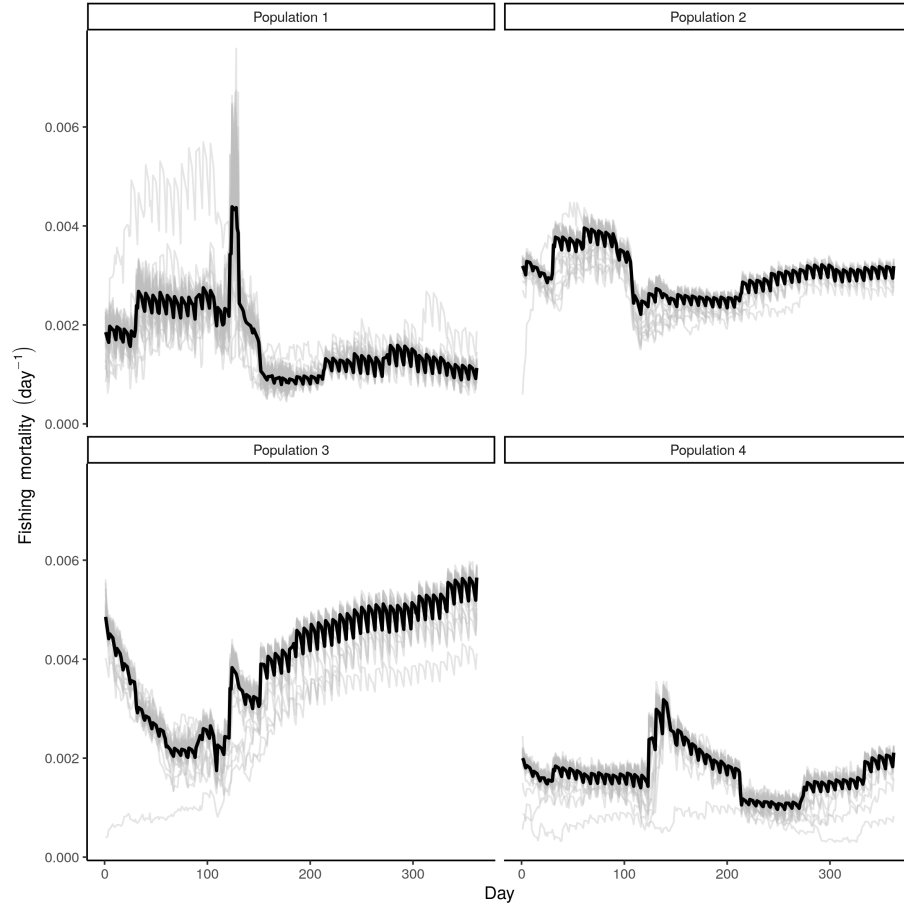


Figure 3: Fishing mortality dynamics - the daily fishing mortalities across the entire spatial domain showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line.

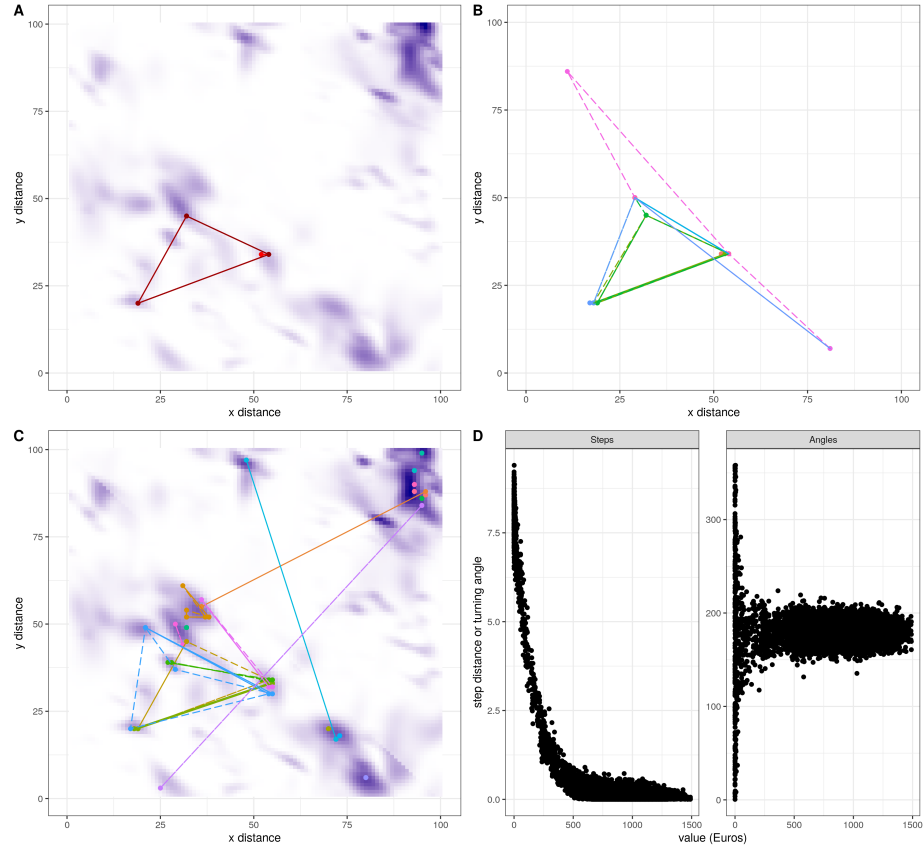


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are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

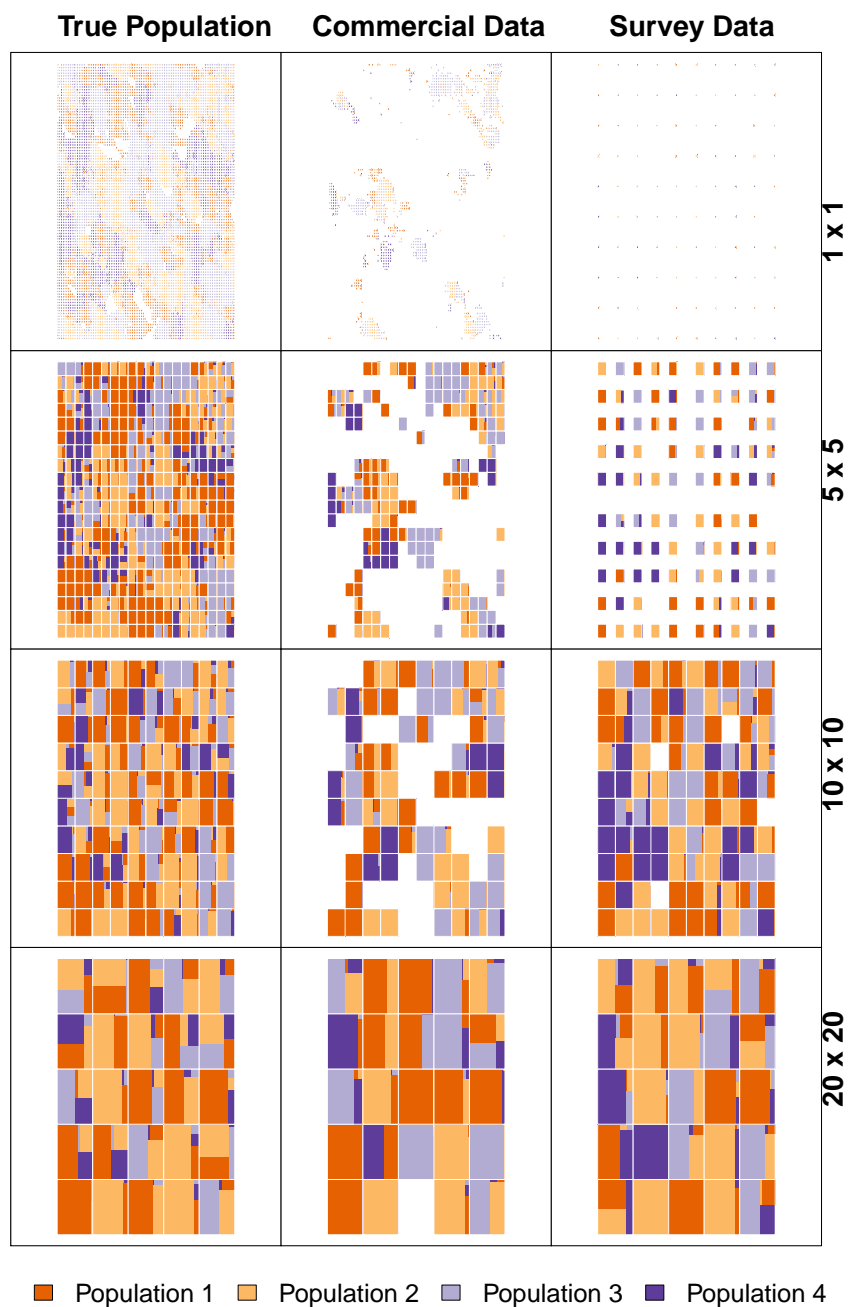


Figure 5: Data aggregation at different spatial resolutions over a ten year period.



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

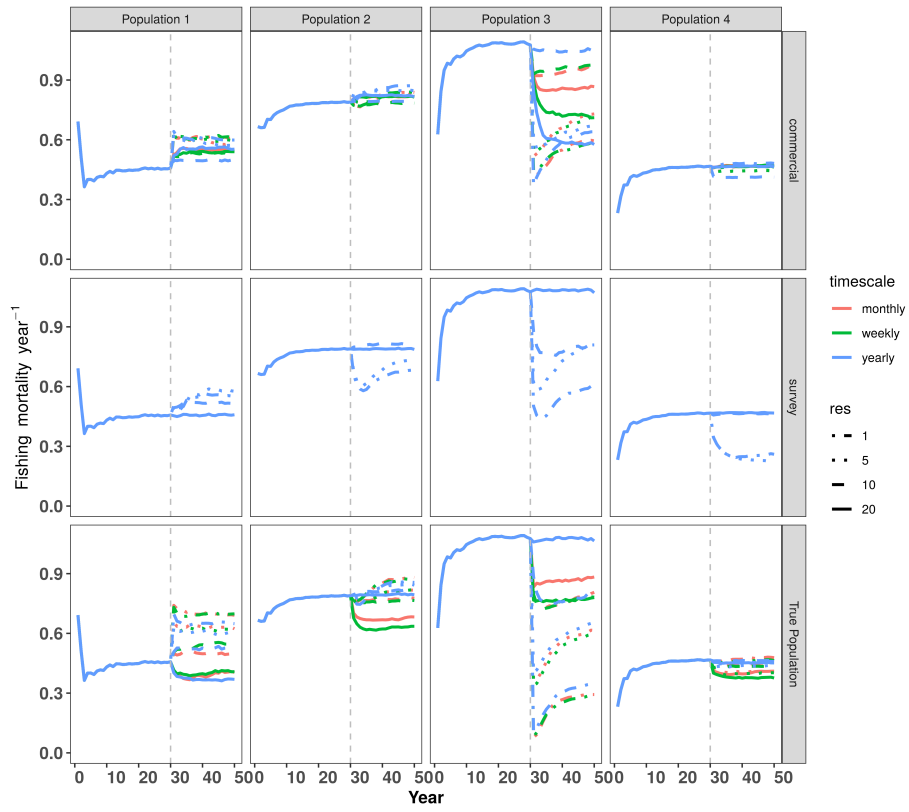


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.



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



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

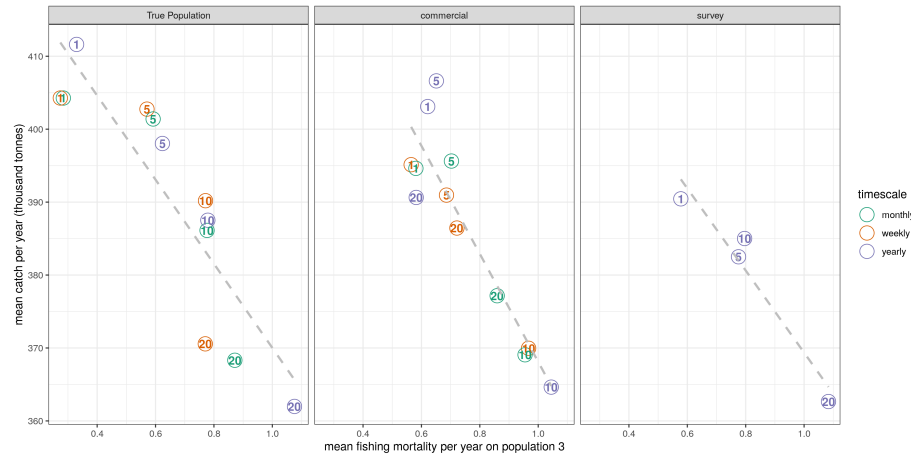


Figure 10: Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the direction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

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