

MixFishSim: 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

^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*

Abstract

Most fisheries exploit a variety of spatially and temporally heterogeneous fish populations using species-unselective gear that can result in unintended, unwanted catch of low quota or protected species. Reducing these unwanted catches is crucial for biological and economic sustainability of ‘mixed fisheries’ and implementation of an ecosystem approach to fishing.

If fisheries are to avoid unwanted catch a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distributions, population movement and how fishers interact with different fish populations. This reflects the fact that data on fish location at high temporal and spatial resolutions is expensive and difficult to collect. Proxies inferred from either scientific surveys or commercial catch data are often used to model distributions, usually with sparse data at limited spatial and temporal resolution.

To understand how data resolution impacts inference on mixed fisheries interactions, we develop a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement

*Corresponding author

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

using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting under an explore-exploit strategy via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

We simulate 50 years of fishing and use the results from the fisheries catch to draw inference on the underlying population structures. We compare this inference to a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying population structures. We i) use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and ii) simulate an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions and assess their effectiveness on reducing catches of a fish population.

We conclude from our simulations that commercial data, while containing bias, provides 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 and using species non-selective fishing gear. In doing so fisheries catch an assemblage of species and may discard over-quota catch when managed by single species quotas and fishers exhaust one or more quota. This may lead to overexploita-

tion of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the ability to maintain fishing mortality within sustainable limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the biological and economic sustainability of fisheries. As such, 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).

Changes to spatial fishing patterns have been proposed as a method to reduce discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). Implementation of avoidance measures is, however, restricted by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management. Understanding the correct scale for spatial measures is crucial for implementation at a resolution that ensures effective management (Dunn et al., 2016) while minimising economic impact. For example, a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species.

Identifying an appropriate scale has been a challenge in the past that has led to ineffectual measures with unintended consequences such as limited impact towards the management objective or increased benthic impact on previously unexploited areas (e.g. the cod closure in the North Sea (Rijnsdorp et al., 2001; Dinmore et al., 2003)). More refined spatial information has since become available through the combination of logbook and Vessel Monitoring System (VMS) data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). Such information is, however, derived from an inherently biased sampling programme, targeted fishing, where fishers establish favoured fishing grounds through an explore-exploit strategy (Bailey et al., 2018) where they

38 search for areas with high catches and then use experience to return to areas
39 where they’ve experienced high catch in the past.

40

41 We ask two fundamental questions regarding spatiotemporal inference de-
42 rived from observational data:

- 43 1. How does sampling-derived data reflects the underlying population struc-
44 tures?
- 45 2. How does data aggregation and source impact on spatial fisheries man-
46 agement measures?

47 To answer these questions we i) develop a simulation model where population
48 dynamics are highly-resolved in space and time. Being known directly rather
49 than inferred from sampling or commercial catch, we can use the population
50 model to validate how inference from fisheries-dependent and fisheries indepen-
51 dent sampling relates to the real population structure in a way we could not
52 with real data. We ii) compare, at different spatial and temporal aggregations,
53 the ‘real population’ distributions to samples from fisheries-dependent and fish-
54 eries independent catches to test if these are a true reflection of the relative
55 density of the populations. We then iii) simulate a fishery closure to protect a
56 species based on different spatial and temporal data aggregations. We use these
57 evaluations to draw inference on the utility of commercial data in supporting
58 management decisions.

59

60 [We find..]

61 2. Materials and Methods

62 A simulation model that is modular and discrete-event based was developed.
63 This approach enables efficient computation by allowing for sub-modules imple-
64 mented on time-scales appropriate to capture the characteristic of the different
65 processes (Figure 1). The following sub-modules were included to capture the

66 full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population
67 movement, 4) fishery dynamics.

68

69 Population dynamics (fishing and natural mortality, growth) operate on a
70 daily time-step, while population movement occurs on a weekly time-step. Re-
71 cruitment takes place periodically each year for a set time duration specified for
72 each population, while the fishing module operates on a tow-by-tow basis (i.e.
73 multiple events a day).

74 In the model system population movement is driven by random (diffusive)
75 and directed (advective) processes and we incorporate characterisation of a num-
76 ber of different fishing fleet dynamics exploiting four fish populations with dif-
77 ferent spatial and population demographics. The following describes the imple-
78 mentation of each of the sub-modules.



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.

79 *2.1. Population dynamics*

80 The basic population level processes are simulated using a modified two-stage
 81 Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont
 82 et al., 2003) occurring at a daily time-step. A daily time-step was chosen to
 83 discretise continuous population processes on a biologically relevant and com-
 84 putationally tractable timescale. Under the population dynamics module pop-
 85 ulation biomass growth and depletion for pre-recruits and recruited fish are
 86 modelled separately as a function of previous recruited biomass, intrinsic popu-
 87 lation growth and recruitment functionally linked to the adult population size.
 88 Biomass for each cell c is incremented each day d as follows (the full parameter
 89 list is detailed in Table 1):

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

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

95

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

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

100 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and
 101 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 and fishing mortality are the sum of those across all fleets and vessels, where $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot B_{c,d,p}$ with fl , v and p the fleet, vessel and population respectively and E and Q fishing effort and catchability.

2.2. Recruitment dynamics

Recruitment is modelled through a function relating the adult biomass to recruits at time of recruitment. In *MixFishSim*, it can be modelled either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

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, or a stochastic Ricker form (Ricker, 1954):

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

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases. In our example application the Beverton-Holt form of stock recruit relationship was used for all populations though either functional form can be chosen.

2.3. Population movement dynamics

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. 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) and we change the parameters to implement different spatial structures for the populations.

The habitat for each of the populations was generated with the *RFSimulate* function of the *RandomFields* R package (Schlatter et al., 2015), that simulates a Gaussian Random Field process given a user defined error model and correlation structure. We define a stationary habitat field and combine with a temporally dynamic thermal tolerance field to imitate two key drivers of population dynamics. Each population was initialised at a single location, and subsequently moved according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature and distance from current cell:

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

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

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

An advection-diffusion process controls population movement, with a time-varying temperature covariate used to change the interaction between time and

154 suitable habitat on a weekly time-step. Each population p was assigned a ther-
 155 mal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population
 156 temperature suitability is defined that:

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

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

160

161 The final process results in a population structure and movement pattern
 162 unique to each species, with population movement occurring on a weekly basis.
 163 The decision to model population movement on a weekly timescale was to reflect
 164 that fish tend to aggregate in species specific locations that have been observed
 165 to last around one to two weeks (Poos and Rijnsdorp, 2007b). Therefore this
 166 process approximated the demographic shifts in fish populations throughout a
 167 year with seasonal spawning patterns (e.g. Figure S5).

168 2.4. Fleet dynamics

169 The fleet dynamics can be broadly categorised into three components; fleet
 170 targeting - that determines the fleet catch efficiency and preference towards a
 171 particular species; trip-level decisions, that determines the initial location to be
 172 fished at the beginning of a trip; and within-trip decisions, determining move-
 173 ment from one fishing spot to another within a trip. Together, these elements
 174 implement an explore-exploit type strategy for individual vessels to maximise
 175 their catch from an unknown resource distribution Bailey et al. (2018). The
 176 decision to use an individual based model for fishing vessels was taken because
 177 fishers are heterogeneous in their location choice behaviour due to different
 178 objectives, risk preference and targeting preference (Van Putten et al., 2012).
 179 Therefore in the simulations fleet dynamics are the productive of individual
 180 experiences rather than pre-defined group dynamics.

181 2.4.1. Fleet targeting

182 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
183 and a population specific efficiency, $Q_{fl,p}$. Thus, the product of these param-
184 eters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential
185 targeting of one population over another. This, in combination with the param-
186 eter choice for the step-function defined below (as well as some randomness from
187 the exploratory fishing process) determined the preference of fishing locations
188 for the fleet. All species prices were kept the same across fleets and seasons.

189 2.4.2. Trip-level decisions

190 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,
191 2015) have confirmed past activity and past catch rates are strong predictors of
192 fishing location choice. For this reason, the fleet dynamics sub-model included a
193 learning component, where a vessel's initial fishing location in a trip was based
194 on selecting from previously successful fishing locations. This was achieved by
195 calculating an expected revenue based on the catches from locations fished in
196 the preceding trip as well as the same month periods in previous years and the
197 travel costs from the port to the fishing grounds, and choosing randomly from
198 the top 75 % of fishing events as defined by the expected profit, that has a
199 seasonal component.

200 2.4.3. Within-trip decisions

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

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

214

215 We use a *Lévy flight* which is a particular form of random walk charac-
 216 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-
 217 ceived a lot of attention in ecological theory in recent years as having shown to
 218 have very similar characteristics as those observed by animals in nature, and
 219 being a near optimum searching strategy for predators pursuing patchily dis-
 220 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,
 221 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a
 222 stochastic search pattern similar to that observed with a lévy flight. However,
 223 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),
 224 with the contention that search patterns may be more simply characterised as
 225 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the
 226 characteristics of the prey field (Sims et al., 2012).

227

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

$$Rev = \sum_{p=1}^P L_p \cdot Pr_p \quad (7)$$

234 where L_p is landings of a population p , and Pr_p price of a population. Here,
 235 when fishing is successful vessels remain in a similar location and continue to
 236 exploit the local fishing grounds. When unsuccessful, they move some distance
 237 away from the current fishing location. The movement distance retains some
 238 degree of stochasticity, that can be controlled separately, but is determined by

239 the relationship:

$$StepL = e^{\log(\beta_1) + \log(\beta_2) - (\log(\frac{\beta_1}{\beta_3}))} * Rev \quad (8)$$

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

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

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

242 where k the concentration parameter from the von Mises distribution that we
 243 correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where max_k
 244 is the maximum concentration value, k , and $RefRev$ is parametrised as for β_3
 245 in the step length function. A realised example of the step length and turning
 246 angle relationships to revenue can be seen at Figure S15.

247 2.4.4. Local population depletion

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

258 2.5. Fisheries independent survey

259 A fisheries-independent survey is simulated where fishing on a regular grid
 260 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. 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

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

3. Parameterisation

3.1. Population models

We parametrised the simulation model for four populations with different demographics; growth rates, natural mortality and recruitment functions (Table 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3, S4) were unique to each population resulting in differently weekly distribution patterns (Figures S5-S7). In addition, each of the populations has two defined spawning areas that result in the populations moving towards these areas in pre-defined weeks (Figure S2) with population-specific movement rates (Table 4). The individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure S9) and consequently different seasonal exploitation patterns (Fishing mortality in Figure S10).

3.2. Fleet parametrisation

The fleets were parametrised to reflect five different characteristic fisheries with unique exploitation dynamics (Table 5). By setting different catchability parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets and hence spatial dynamics. The stochasticity in the random walk process

ensures that within a fleet different vessels have slightly different spatial distributions based on individual experience. The step function was parametrised dynamically within the simulations as the maximum revenue obtainable was not known beforehand. This was implemented so that vessels take smaller steps when fishing at a location that yields landings value in the top 90th percentile of the value experienced in that year so far (as defined per fleet in Table 5).

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

3.3. Survey settings

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

3.4. Example research question

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

317 times a day per vessel and five days a week, while population movement is every
318 week.

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

323

324 The following steps are undertaken to determine closures:

- 325 1. Extract data source
- 326 2. Aggregate according to desired spatial and temporal resolution
- 327 3. Interpolate across entire area at desired resolution using simple kriging
328 using the *interp* function from the R package *akima* (Akima, 2006).
- 329 4. Close area covering top 5 % of catch rates

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

- 331 • **data types:** commercial logbook data, survey data and 'real population',
- 332 • **temporal resolutions:** weekly, monthly and yearly closures,
- 333 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 334 • **closure basis:** highest 5 % of catch rates for the protected species

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

337 4. Results

338 4.1. Simulation dynamics

It can be seen from a single vessels movements during a trip that the vessel exploits four different fishing grounds, three of them multiple times (Figure S11), while across several trips fishing grounds that are further apart are fished (Figure

S12). These different locations relate to areas where the highest revenue were experienced, as shown by Figure S13, where several trips for the vessel overlaid on the revenue field, i.e.

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

339 Vessels from the same fleet (and therefore targeting preference) exploit sim-
 340 ilar but slightly different fishing grounds depending on their own personal ex-
 341 perience during the explore phase of the fishery (Figure S14), that is the result
 342 of the randomness in the correlated random walk step function, with distance
 343 moved during the exploitation phase and the direction stochastically related to
 344 the revenue experienced on the fishing ground (Figure S15).

345 4.2. How does sampling-derived data reflect the underlying population structure?

346 In order to answer this question we compare different spatial and temporal
 347 aggregations of the 'real population' distributions to:

- 348 a) **fisheries-independent data:** the inferred population from a fixed-site
 349 sampling survey design as commonly used for fisheries monitoring pur-
 350 poses;
- 351 b) **fisheries-dependent data:** the inferred population from our fleet model
 352 that includes fishery-induced sampling dynamics.

353 Figure 2 shows the aggregated catch composition from each of the data
 354 sources over a ten-year period (to average seasonal patterns) at different spa-
 355 tial resolutions. The finer spatial grid for the real population (top left) and
 356 commercial data (top middle) show visually similar patterns, though there are
 357 large unsampled areas in the commercial data from a lack of fishing activity
 358 (particularly in the lower left part of the sampling domain). The survey data at
 359 this spatial resolution displays very sparse information about the spatial distri-
 360 butions of the populations. The slightly aggregated data on a 5 x 5 grid shows
 361 similar patterns and, while losing some of the spatial detail, there remains good
 362 consistency between the 'real population' and the commercial data. Survey data

363 starts to pick out some of the similar patterns as the other data sources, but
364 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and
365 20 x 20 grid lose a significant amount of information about the spatial resolu-
366 tions for all data sources, and some differences between the survey, commercial
367 and 'real population' data emerge.

368

369 Figure 3 shows the consequences of different temporal aggregations of the
370 data over a ten-year period, with weekly (top), monthly (middle) and yearly
371 (bottom) catch compositions from across an aggregated 20 x 20 area. By com-
372 parison to the 'real population', the monthly aggregation captures the major
373 patterns seen in the weekly data, albeit missing more subtle differences. The
374 yearly data results in a constant catch pattern due to the aggregation process
375 (sometimes known as an aggregation bias). The commercial data on a weekly
376 basis shows some of the same patterns as the 'real population', though the first
377 species (in red) is less well represented and some weeks are missing catches
378 from the area. The monthly data shows some consistency between the 'real
379 population' and commercial data for species 2 - 4, though species 1 remains
380 under-represented. On an annual basis, interestingly the commercial data un-
381 der represents the first species (in red) while the survey over represents species
382 1. This is likely due to the biases in commercial sampling, with the fisheries
383 not targeting the areas where species 1 are present, and the biases in the survey
384 sampling from over representation of the spatial distribution.

385 *4.3. How does data aggregation and source impact on spatial fisheries manage-* 386 *ment measures?*

387 We implemented a spatial closure using the different data sources and spatial
388 and temporal aggregations as outlined in the protocol in Section 3.4. We used
389 this to assess the efficacy of a closure in reducing fishing mortality on species 3,
390 given availability of data and its use at different resolutions in order to evaluate
391 the trade-offs in data sources.

392 The trend in fishing mortality for each species show that in most cases the

fishery closure was successful in reducing fishing mortality on the species of interest (species 3; Figure 4), though interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries "adapted" to the closures and fishing mortality increased again somewhat. The exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all data sources. As expected, closures based on the "known" population distribution were most effective, with differing degrees of success using the commercial data. Fishing mortality rates on the other species changed in different proportions, depending on whether the displaced fishing effort moved to areas where the populations were found in greater or lesser density.

A regression tree (using the R package REEMtree (Sela and Simonoff, 2012)) highlights that the factor most contributing to differences in fishing mortality before and after the closure was the population (72 % showing that the closures were effective for population 3), followed by data resolution (21 %), data type (7 %) with the least important factor the timescale (< 1 %). In general the finer the spatial resolution of the data used the greater reduction in fishing mortality for population 3 after the closures (Figure 5). The notable outliers are the commercial 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 S17) that may have consequences in terms of restricting the fishery in a much larger area than necessary.

420 5. Discussion

421 Our study evaluates the importance of data scaling and considers poten-
422 tial bias introduced through data aggregation when using fisheries data to infer
423 spatiotemporal dynamics of fish populations. Understanding how fishers ex-
424 ploit multiple heterogeneously distributed fish populations with different catch
425 limits or conservation status requires detailed understanding of the overlap of
426 resources; this is difficult to achieve using conventional modelling approaches
427 due to species targeting in fisheries resulting in preferential sampling (Martínez-
428 Minaya et al., 2018). Often data are aggregated or extrapolated which requires
429 assumptions about the spatial and temporal scale of processes. Our study ex-
430 plores the assumptions behind such aggregation and preferential sampling to
431 identify potential impacts on management advice. With modern management
432 approaches increasingly employing more nuanced spatiotemporal approaches in
433 order to maximise productivity while taking account of both the biological and
434 human processes operating on different time-frames (Dunn et al., 2016), un-
435 derstanding assumptions behind the data used - increasingly a combination of
436 logbook and positional information from vessel monitoring systems - is vital to
437 ensure measures are effective.

438 439 5.1. Simulation dynamics

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

445
446 Our approach is unique in that it captures fine scale population and fish-
447 ery dynamics and their interaction in a way not usually possible with real data
448 and thus not usually considered in fisheries simulations. While other simulation

frameworks seek to model individual vessel dynamics based on inferred dynamics from VMS and logbook records (Bastardie et al., 2010), or as a system to identify measures to meet particular management goals (Bailey et al., 2018), 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. This offers the advantage that larger scale fishery patterns are emergent properties of the system and results can be compared to those obtained under a statistical modelling framework.

Typically, simulation models that treat fish as individuals are focussed on exploring the inter- and intra- specific interactions among fish populations (e.g. OSMOSE Shin et al. (2004)) in order to understand how they vary over space and time. Our focus was on understanding the strengths and limitations of inference from catch data obtained through commercial fishing activity with fleets exploiting multiple fish populations and realising catch distributions that may differ from the underlying populations. As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014), while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way. In this way 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 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.

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

From our simulations spatial disaggregation was more important than the temporal disaggregation of the commercial data. This reflects the fact that there was greater spatial heterogeneity over the spatial domain than experienced in individual locations over the course of the year (Figure S9). This indicates that fixed closures, at the right resolution, when based on commercially derived data have the potential to reduced fishing mortality. The likely cost of poor spatial and temporal resolution is associated with reduced effectiveness and potentially closing fishing opportunities for other fisheries.

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

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

509 5.4. *Model assumptions and caveats*

510 We model the population and fleet dynamic processes in order to draw in-
511 ference on the importance of data scale and aggregation in understanding and
512 managing mixed fisheries and their impact on multiple fish populations. In do-
513 ing so, we have necessarily had to make a number of simplifying assumptions.

514
515 Fish populations in our simulations move in pre-defined timescales and ac-
516 cording to fixed habitat preferences and temperature gradients. Our assump-
517 tions in parametrising the model (movement rates, temperature tolerances) will
518 have a direct impact on our conclusions on the relative importance of spatial
519 and temporal processes. These assumptions could be explored in a future study
520 by varying the parameters and assessing the robustness of our conclusions.

521
522 In addition, we have assumed that fishing vessels are not restricted by quota
523 and therefore discarding of species for which vessels have no quota or that are
524 unwanted is not taken into account. This is likely to be a significant source of
525 bias in any inference using commercial data and should also be explored.

527 5.5. *Future application for framework*

528 We consider that the increased availability of high resolution catch and lo-
529 cational information from commercial fisheries will require it to be a key source
530 of data for ensuring management is implemented at the right scale in future.
531 For example, identifying hot-spots for bycatch reduction or identifying spatial
532 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
533 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
534 potential to test some of the assumptions behind the modelling approaches in
535 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
536 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
537 els under different data generation processes as exemplified by Stock et al. (2019)).

538

539 Other novel applications of our framework could be; testing different survey
540 designs given multiple species and data generating assumptions; commercial in-
541 dex standardisation methods and approaches and understanding of appropriate
542 scales and data aggregations; exploring assumptions about the distribution of
543 natural mortality and fishing mortality throughout the year and importance of
544 capturing in-year dynamics in estimating stock status; at sea sampling scheme
545 designs to deliver unbiased estimates of population parameters; testing the abil-
546 ity of commonly employed fleet dynamics models such as Random Utility Models
547 to capture finescale dynamics and understand their importance.

548

549 **6. Conclusions**

550 Bigger picture stuff:: LO, increasing desire for more nuanced spatiotemp
551 mgmt... Wider applicability: birds, wildlife ??

552 Study shows

553

554 This is important because

555

556 How we might apply this in future

557

558 **Abbreviations**

559 Detail any unusual ones used.

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566 **Appendices**

Table 1: Description of variables for population dynamics sub-module

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

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

Variable	Meaning	Units
Population movement dynamics		
<i>Habitat model</i>		
a	b	c
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell in week	°C
μ_p	Mean of the thermal tolerance for population	°C
σ_p^2	Standard deviation of thermal tolerance for the population	°C
<i>Population movement model</i>		
λ	decay rate for population movement	-
$Hab_{c,p}^2$	Square of habitat suitability for cell c and population p	-
$Tol_{c,p,wk}$	Thermal tolerance for population p in cell c at week wk	-
d_{IJ}	euclidean distance between cell I and cell J	-

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

Variable	Meaning	Units
Short-term fleet dynamics		
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg ⁻¹
StepL	Step length for vessel	euclidean distance
Br	Bearing	degrees
k	Concentration parameter for Von mises distribution	-
β_1	shape parameter for step function	-
β_2	shape parameter for step function	-
β_3	shape parameter for step function	-

Table 4: Population dynamics and movement parameter setting

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

Table 5: Fleet dynamics parameter setting

Parameter	Fleet	Fleet	Fleet	Fleet	Fleet
	1	2	3	4	5
Targeting preferences	pop	pop	-	pop 4	pop
	2/4	1/3			2/3
Price Pop1	100	100	100	100	100
Price Pop2	200	200	200	200	200
Price Pop3	350	350	350	350	350
Price Pop4	600	600	600	600	600
Q Pop1	0.01	0.02	0.02	0.01	0.01
Q Pop2	0.02	0.01	0.02	0.01	0.03
Q Pop3	0.01	0.02	0.02	0.01	0.02
Q Pop4	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_3	Q90	Q90	Q85	Q90	Q80
step function $rate$	20	30	25	35	20
Past Knowledge	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios. Results show the fishing mortality before the closure (f.before) and after the closure (f.after) and the percentage change in f (f.change). The results are ordered by most effective scenario first, least effective last.)

scenario	metric	pop	f.before	f.after	f.change	timescale	basis	data_type	resolution
9	F	spp_3	1.08	0.29	-73.47	weekly	high_pop	real_pop	1.00
10	F	spp_3	1.08	0.29	-72.94	monthly	high_pop	real_pop	1.00
11	F	spp_3	1.08	0.35	-68.04	yearly	high_pop	real_pop	1.00
45	F	spp_3	1.08	0.58	-46.70	yearly	high_pop	commercial	20.00
1	F	spp_3	1.08	0.58	-46.21	weekly	high_pop	commercial	1.00
23	F	spp_3	1.08	0.59	-45.27	weekly	high_pop	real_pop	5.00
2	F	spp_3	1.08	0.59	-45.06	monthly	high_pop	commercial	1.00
7	F	spp_3	1.08	0.60	-44.48	yearly	high_pop	survey	1.00
24	F	spp_3	1.08	0.61	-43.20	monthly	high_pop	real_pop	5.00
3	F	spp_3	1.08	0.64	-40.82	yearly	high_pop	commercial	1.00
25	F	spp_3	1.08	0.65	-39.94	yearly	high_pop	real_pop	5.00
17	F	spp_3	1.08	0.67	-38.11	yearly	high_pop	commercial	5.00
15	F	spp_3	1.08	0.71	-34.38	weekly	high_pop	commercial	5.00
43	F	spp_3	1.08	0.71	-34.31	weekly	high_pop	commercial	20.00
16	F	spp_3	1.08	0.73	-32.58	monthly	high_pop	commercial	5.00
51	F	spp_3	1.08	0.78	-27.92	weekly	high_pop	real_pop	20.00
37	F	spp_3	1.08	0.78	-27.76	weekly	high_pop	real_pop	10.00
39	F	spp_3	1.08	0.79	-26.98	yearly	high_pop	real_pop	10.00
38	F	spp_3	1.08	0.81	-25.47	monthly	high_pop	real_pop	10.00
21	F	spp_3	1.08	0.81	-25.21	yearly	high_pop	survey	5.00
35	F	spp_3	1.08	0.81	-25.05	yearly	high_pop	survey	10.00
44	F	spp_3	1.08	0.87	-19.91	monthly	high_pop	commercial	20.00
52	F	spp_3	1.08	0.88	-18.39	monthly	high_pop	real_pop	20.00
30	F	spp_3	1.08	0.96	-11.06	monthly	high_pop	commercial	10.00
29	F	spp_3	1.08	0.98	-9.80	weekly	high_pop	commercial	10.00
31	F	spp_3	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	spp_3	1.08	1.06	-1.64	yearly	high_pop	real_pop	20.00
49	F	spp_3	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

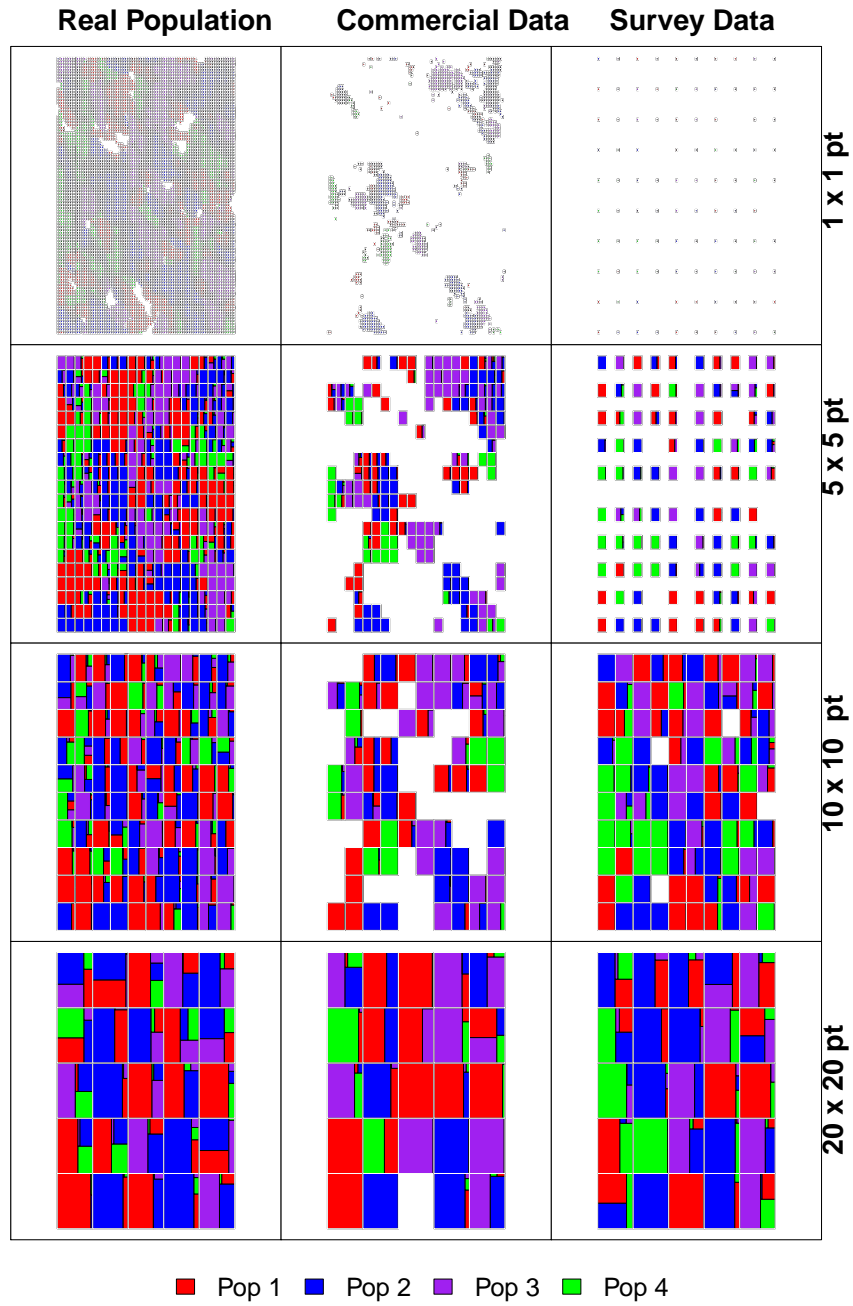


Figure 2: Data aggregation at different spatial resolutions over a ten year period

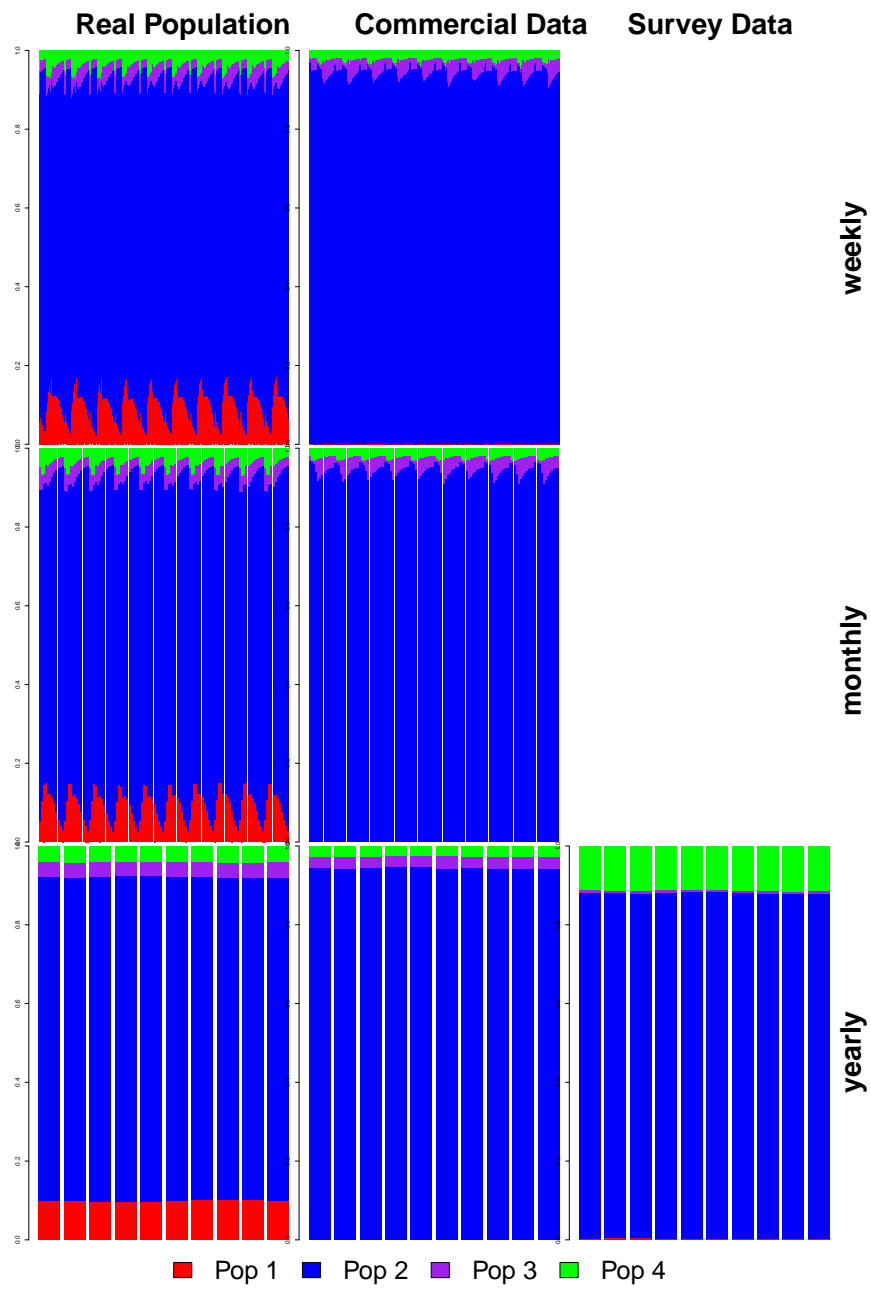


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

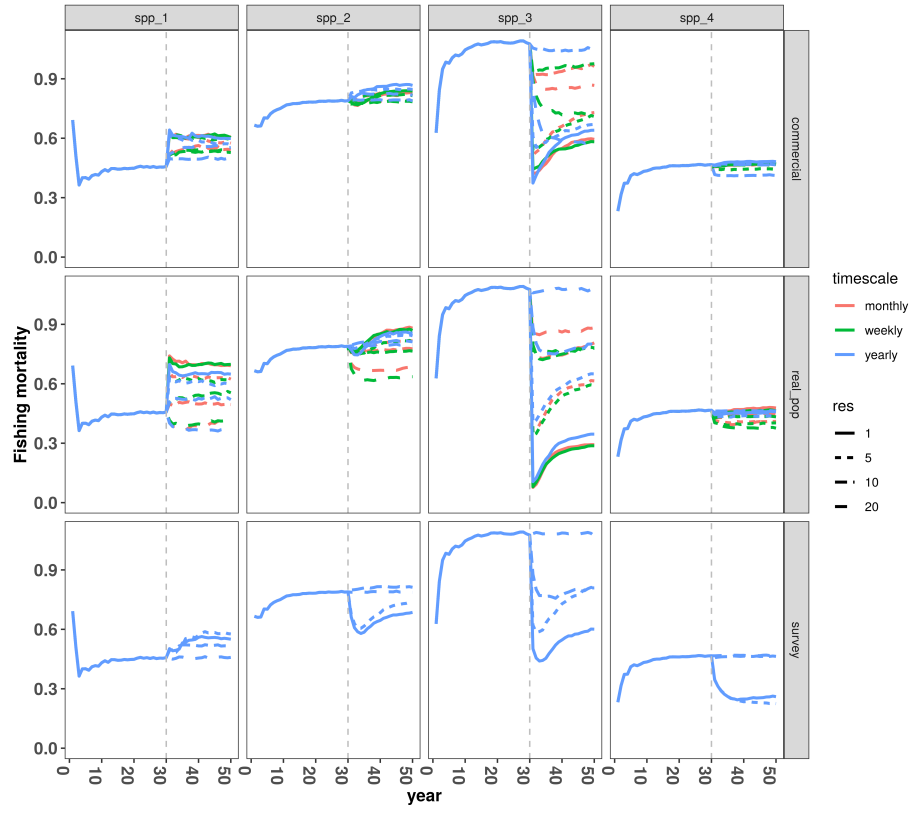


Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

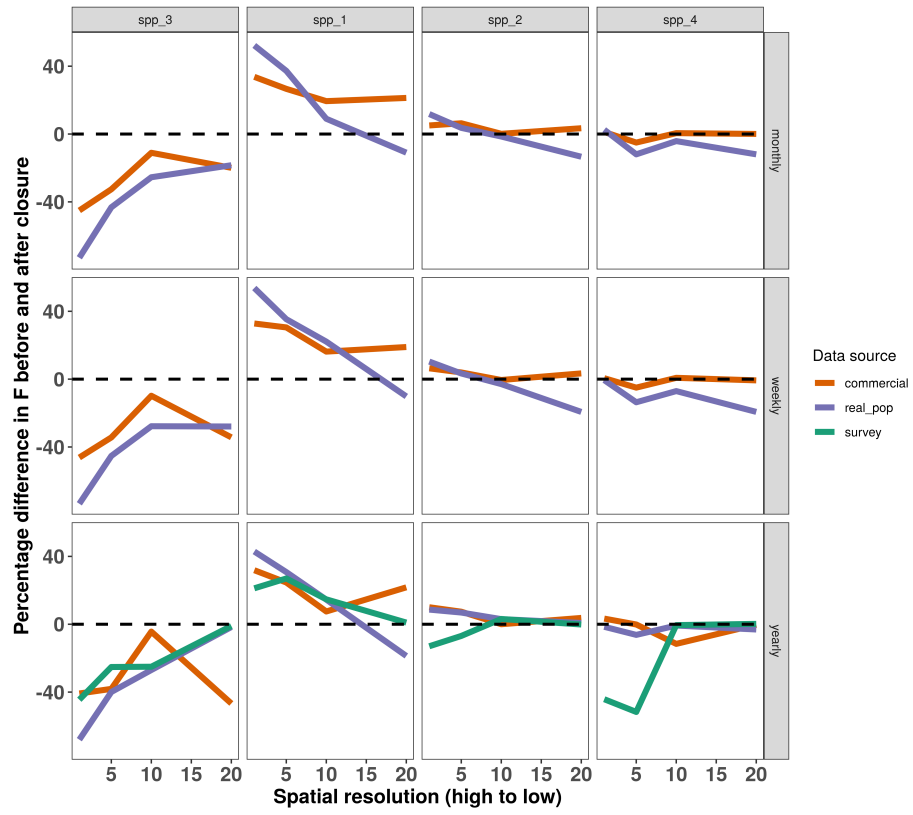


Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

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