

# *MixFishSim*: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder<sup>a,b,\*</sup>, C  il  n Minto<sup>a</sup>, Jean-Marc Guarini<sup>c</sup>, Jan Jaap Poos<sup>d</sup>

<sup>a</sup>*Galway-Mayo Institute of Technology (GMIT), Dublin Road, Galway, Ireland*

<sup>b</sup>*Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, UK*

<sup>c</sup>*Sorbonne Universit  , Faculty of Sciences, 4 Place Jussieu, 75005 Paris, France*

<sup>d</sup>*Wageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands*

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## 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

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\*Corresponding author

Email address: [paul.dolder@gmit.ie](mailto: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.

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.

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 overexploitation 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;

31 Dinmore et al., 2003)). More refined spatial information has since become avail-  
 32 able through the combination of logbook and Vessel Monitoring System (VMS)  
 33 data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al.,  
 34 2016) and more real-time spatial management has been possible (e.g. Holmes  
 35 et al., 2011). Such information is, however, derived from an inherently biased  
 36 sampling programme, targeted fishing, where fishers establish favoured fishing  
 37 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  $\rho$  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.  $\alpha_d$  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  $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot D_{c,d,p}$  with  $fl$ ,  $v$  and  $p$  the fleet, vessel and population respectively and  $E$  and  $Q$  fishing effort and catchability of the gear, and  $D$  is the density of the population at the location fished.

## 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 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  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB) required to produce half the maximum stock size,  $S$  current stock size and  $\sigma^2$  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  $\alpha$  is the maximum productivity per spawner and  $\beta$  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.



125 We first defined a Gaussian random field process,  $\{S(c) : c \in \mathbb{R}^2\}$ , where  
 126 for any set of cells  $c_1, \dots, c_n$ , the joint distribution of  $S = \{S(c_1), \dots, S(c_n)\}$   
 127 is multivariate Gaussian with a *Matérn* covariance structure, where the corre-  
 128 lation strength weakens with distance. This enables us to model the spatial  
 129 autocorrelation observed in animal populations where density is more similar  
 130 in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the  
 131 parameters to implement different spatial structures for the populations.

132  
 133 The habitat for each of the populations was generated with the *RFSimulate*  
 134 function of the *RandomFields* R package (Schlatter et al., 2015), that simulates  
 135 a Gaussian Random Field process given a user defined error model and cor-  
 136 relation structure. We define a stationary habitat field and combine with a  
 137 temporally dynamic thermal tolerance field to imitate two key drivers of pop-  
 138 ulation dynamics. Each population was initialised at a single location, and  
 139 subsequently moved according to a probabilistic distribution based on habitat  
 140 suitability (represented by the normalised values from the GRFs), temperature  
 141 and distance from current cell:

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

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

146  
 147 During pre-defined weeks of the year the habitat quality is modified with  
 148 user-defined spawning habitat locations, resulting in each population having  
 149 concentrated areas where spawning takes place. In the simulations the popu-  
 150 lations move towards these cells in the weeks prior to spawning, resulting in  
 151 directional movement towards the spawning grounds.

152

153 An advection-diffusion process controls population movement, with a time-  
 154 varying temperature covariate used to change the interaction between time and  
 155 suitable habitat on a weekly time-step. Each population  $p$  was assigned a ther-  
 156 mal tolerance with mean,  $\mu_p$  and variance,  $\sigma_p^2$  so that each cell and population  
 157 temperature suitability is defined that:

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

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

161

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

#### 169 2.4. Fleet dynamics

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

180 Therefore in the simulations fleet dynamics are the productive of individual  
181 experiences rather than pre-defined group dynamics.

#### 182 2.4.1. Fleet targeting

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

#### 190 2.4.2. Trip-level decisions

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

#### 201 2.4.3. Within-trip decisions

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

about which there is uncertain knowledge (Viswanathan et al., 1999). In a random walk, movement is a stochastic process through a series of steps. These steps have a length, and a direction that can either be equal in length or take some other functional form. The direction of the random walk was also correlated (known as ‘persistence’) providing some overall directional movement (Codling et al., 2008).

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

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 recent fishing success, measured as the summed value of fish caught (revenue,  $Rev$ ),

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

where  $L_p$  is landings of a population  $p$ , and  $Pr_p$  price of a population. 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:

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

Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function 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  $Br_{t-1} < 180, Br_t = 180 + \sim vm[(0, 360), k]$   
 $Br_{t-1} > 180, Br_t = 180 - \sim vm[(0, 360), k]$

where  $k$  the concentration parameter from the von Mises distribution that we correlate with the revenue so that  $k = (Rev + 1/RefRev) * max_k$ , where  $max_k$  is the maximum concentration value,  $k$ , and  $RefRev$  is parametrised as for  $\beta_3$  in the step length function. A realised example of the step length and turning angle relationships to revenue can be seen at Figure S15.

#### 2.4.4. Local population depletion

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

## 259 2.5. Fisheries independent survey

260 A fisheries-independent survey is simulated where fishing on a regular grid  
261 begins each year at the same time for a given number of stations (a fixed station  
262 survey design). Catches of the populations at each station are recorded but not  
263 removed from the population. This provides a fishery independent snapshot  
264 of the populations at a regular spatial intervals each year, similar to scientific  
265 surveys undertaken by fisheries research agencies.

## 267 2.6. Software

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

271

# 272 3. Parameterisation

## 273 3.1. Population models

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

### 284 3.2. Fleet parametrisation

285 The fleets were parametrised to reflect five different characteristic fisheries  
286 with unique exploitation dynamics (Table 5). By setting different catchability  
287 parameters ( $Q_{fl,p}$ ) we create different targeting preferences between the fleets  
288 and hence spatial dynamics. The stochasticity in the random walk process  
289 ensures that within a fleet different vessels have slightly different spatial dis-  
290 tributions based on individual experience. The step function was parametrised  
291 dynamically within the simulations as the maximum revenue obtainable was  
292 not known beforehand. This was implemented so that vessels take smaller steps  
293 when fishing at a location that yields landings value in the top 90th percentile  
294 of the value experienced in that year so far (as defined per fleet in Table 5).

295  
296 With increasing probability throughout the simulation, fishing locations were  
297 chosen based on experience of profitable catches built up in the same month from  
298 previous years and from the previous trip. 'Profitable' in this context was de-  
299 fined as the locations where the top 70 % of expected profit would be found  
300 given previous trips revenue and cost of movement to the new fishing location.  
301 This probability was based on a logistic sigmoid function with a lower asymp-  
302 tote of 0 and upper asymptote of 0.95, and a growth rate that ensures the upper  
303 asymptote (where decisions are mainly based on past knowledge) is reached ap-  
304 proximately halfway through the simulation.

### 306 3.3. Survey settings

307 The survey simulation was set up with a fixed gridded station design with  
308 100 stations fished each year, starting on day 92 and ending on day 112 (5  
309 stations per day) with same catchability parameters for all populations ( $Q_p =$   
310 1). This approximates a real world survey design with limited seasonal and  
311 spatial coverage.

### 312 3.4. Example research question

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

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

324

325 The following steps are undertaken to determine closures:

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

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

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

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



## 338 4. Results

### 339 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.

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

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

### 346 4.2. How does sampling-derived data reflect the underlying population structure?

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

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

354 Figure 2 shows the aggregated catch composition from each of the data  
355 sources over a ten-year period (to average seasonal patterns) at different spa-  
356 tial resolutions. The finer spatial grid for the real population (top left) and  
357 commercial data (top middle) show visually similar patterns, though there are

358 large unsampled areas in the commercial data from a lack of fishing activity  
 359 (particularly in the lower left part of the sampling domain). The survey data at  
 360 this spatial resolution displays very sparse information about the spatial distri-  
 361 butions of the populations. The slightly aggregated data on a 5 x 5 grid shows  
 362 similar patterns and, while losing some of the spatial detail, there remains good  
 363 consistency between the 'real population' and the commercial data. Survey data  
 364 starts to pick out some of the similar patterns as the other data sources, but  
 365 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and  
 366 20 x 20 grid lose a significant amount of information about the spatial resolu-  
 367 tions for all data sources, and some differences between the survey, commercial  
 368 and 'real population' data emerge.

369

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

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

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

393 The trend in fishing mortality for each species show that in most cases the  
394 fishery closure was successful in reducing fishing mortality on the species of in-  
395 terest (species 3; Figure 4), though interestingly the largest reductions in fishing  
396 mortality happened immediately after the closures, following which the fisheries  
397 "adapted" to the closures and fishing mortality increased again somewhat. The  
398 exception to the success was the closures implemented based on the coarsest  
399 spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all  
400 data sources. As expected, closures based on the "known" population distribu-  
401 tion were most effective, with differing degrees of success using the commercial  
402 data. Fishing mortality rates on the other species changed in different propor-  
403 tions, depending on whether the displaced fishing effort moved to areas where  
404 the populations were found in greater or lesser density.

405  
406 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))  
407 highlights that the factor most contributing to differences in fishing mortality  
408 before and after the closure was the population (72 % showing that the closures  
409 were effective for population 3), followed by data resolution (21 %), data type  
410 (7 %) with the least important factor the timescale (< 1 %). In general the finer  
411 the spatial resolution of the data used the greater reduction in fishing mortality  
412 for population 3 after the closures (Figure 5). The notable outliers are the com-  
413 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly  
414 timescale, where closures were nearly as effective as the fine-scale resolution. In  
415 this case the closures were sufficiently large to protect a core area of the habitat  
416 for the population, but this was achieved in a fairly crude manner by closing a

417 large area - including area where the species was not found (Figure S17) that  
418 may have consequences in terms of restricting the fishery in a much larger area  
419 than necessary.

420

## 421 5. Discussion

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

439

### 440 5.1. Simulation dynamics

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

445 the effectiveness of a spatial closure given those assumptions.

446

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

458

459 Typically, simulation models that treat fish as individuals are focussed on  
460 exploring the inter- and intra- specific interactions among fish populations (e.g.  
461 OSMOSE Shin et al. (2004)) in order to understand how they vary over space  
462 and time. Our focus was on understanding the strengths and limitations of  
463 inference from catch data obtained through commercial fishing activity with  
464 fleets exploiting multiple fish populations and realising catch distributions that  
465 may differ from the underlying populations. As such, we favoured a minimum  
466 realistic model of the fish populations (Plagányi et al., 2014), while incorporating  
467 detailed fishing dynamics that take account of different drivers in a mechanistic  
468 way. In this way we take account of heterogeneity in fleet dynamics due to  
469 different preferences and drivers similarly to other approaches (Fulton et al.,  
470 2011), but at an individual vessel rather than fleet level. We do not explicitly  
471 define fleets as rational profit maximisers at the outset, but consider there are  
472 several stages to development of the fishery; information gathering through  
473 search where the resource location is not known, followed by individual learnt  
474 behaviour of profitable locations. This provides a realistic model of how fishing  
475 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.

Our simulation shows that, despite biases introduced through the fishing process, the commercially derived data could still inform on the key spatial patterns in the community structures where the fisheries occurred, which was spatially limited due to the “hotspots” of commercially valuable species being fished. Similarly, despite the even spatial coverage the survey was able to capture some of the same spatial patterns as the ‘real population’, but missed others due to gaps between survey stations limiting spatial and temporal coverage. This provides a challenge when modelling unsampled areas in inferring species distribution maps, though these limitations may be overcome by understanding the relationship between the species and habitat covariates where these are known at unsampled locations (Robinson et al., 2011).

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

From our simulations spatial disaggregation was more important than the temporal disaggregation of the commercial data. This reflects the fact that there was greater spatial heterogeneity over the spatial domain than experienced in 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

505 and temporal resolution is associated with reduced effectiveness and potentially  
506 closing fishing opportunities for other fisheries.

507

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

517

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

#### 523 *5.4. Model assumptions and caveats*

524 We model the population and fleet dynamic processes to draw inference on  
525 the importance of data scale and aggregation in understanding and managing  
526 mixed fisheries and their impact on multiple fish populations. In doing so, we  
527 have necessarily had to make a number of simplifying assumptions.

528

529 Fish populations in our simulations move in pre-defined timescales and ac-  
530 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).  
531 Our assumptions in parametrising the model (movement rates, temperature tol-  
532 erances) will have a direct impact on our conclusions on the relative importance  
533 of spatial and temporal processes. These assumptions could be explored in a  
534 future study by varying the parameters and assessing the robustness of our con-

535 clusions. For our example application we have chosen movement rates to reflect  
536 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

537

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

546

#### 547 5.5. Future applications of MixFishSim

548 We consider that the increased availability of high resolution catch and lo-  
549 cational information from commercial fisheries will require it to be a key source  
550 of data for ensuring management is implemented at the right scale in future.  
551 For example, identifying hot-spots for bycatch reduction or identifying spatial  
552 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,  
553 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the  
554 potential to test some of the assumptions behind the modelling approaches in  
555 identifying such hotspots and indeed behind spatiotemporal modelling in gen-  
556 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-  
557 els under different data generation processes as exemplified by Stock et al. (2019)).

558

559 Other novel applications of our framework could be; testing different sur-  
560 vey designs given multiple species and data generating assumptions (Xu et al.,  
561 2015); commercial index standardisation methods and approaches and under-  
562 standing of appropriate scales and data aggregations and non-proportionality  
563 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);  
564 exploring assumptions about the distribution of natural mortality and fishing



mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 2013); at sea sampling scheme designs to deliver unbiased estimates of population parameters (Cotter and Pilling (2007); Kimura and Somerton (2006); adaptive management (Walters, 2007; Dunn et al., 2016); testing the ability of commonly employed fleet dynamics models such as Random Utility Models to capture fine scale dynamics and understand their importance (Girardin et al. (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).

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

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

## Abbreviations

Detail any unusual ones used.

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## Appendices

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

Variable	Meaning	Units
<b>Population dynamics</b>		
<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 <sup>-1</sup>
$\rho$	Brody's growth coefficient	yr <sup>-1</sup>
$Wt_R$	Weight of a fully recruited fish	kg
$Wt_{R-1}$	Weight of a pre-recruit fish	kg
$\alpha_d$	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
<b>Recruitment dynamics</b>		
$\tilde{R}_{c,d}$	is the recruitment in cell $c$ for day $d$	$d^{-1}$
$B_{c,d}$	is the Biomass in cell $c$ for day $d$	$d^{-1}$
$\alpha$	the maximum recruitment rate	kg
$\beta$	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
<b>Population movement dynamics</b>		
<i>Habitat model</i>		
a	b	c
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell in week	°C
$\mu_p$	Mean of the thermal tolerance for population	°C
$\sigma_p^2$	Standard deviation of thermal tolerance for the population	°C
<i>Population movement model</i>		
$\lambda$	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
<b>Short-term fleet dynamics</b>		
$Rev$	Revenue from fishing tow	€
$L_p$	Landings of population $p$	kg
$Pr_p$	Average price of population $p$	€ kg <sup>-1</sup>
StepL	Step length for vessel	euclidean distance
Br	Bearing	degrees
$k$	Concentration parameter for Von mises distribution	-
$\beta_1$	shape parameter for step function	-
$\beta_2$	shape parameter for step function	-
$\beta_3$	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 $\nu$	1/0.015	1/0.05	1/0.01	1/0.005
Matérn $\kappa$	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 $\lambda$	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 $\sigma^2$	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				
$\mu$	12	15	17	14
$\sigma^2$	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 $\beta_1$	1	2	1	2	3
step function $\beta_2$	10	15	8	12	7
step function $\beta_3$	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



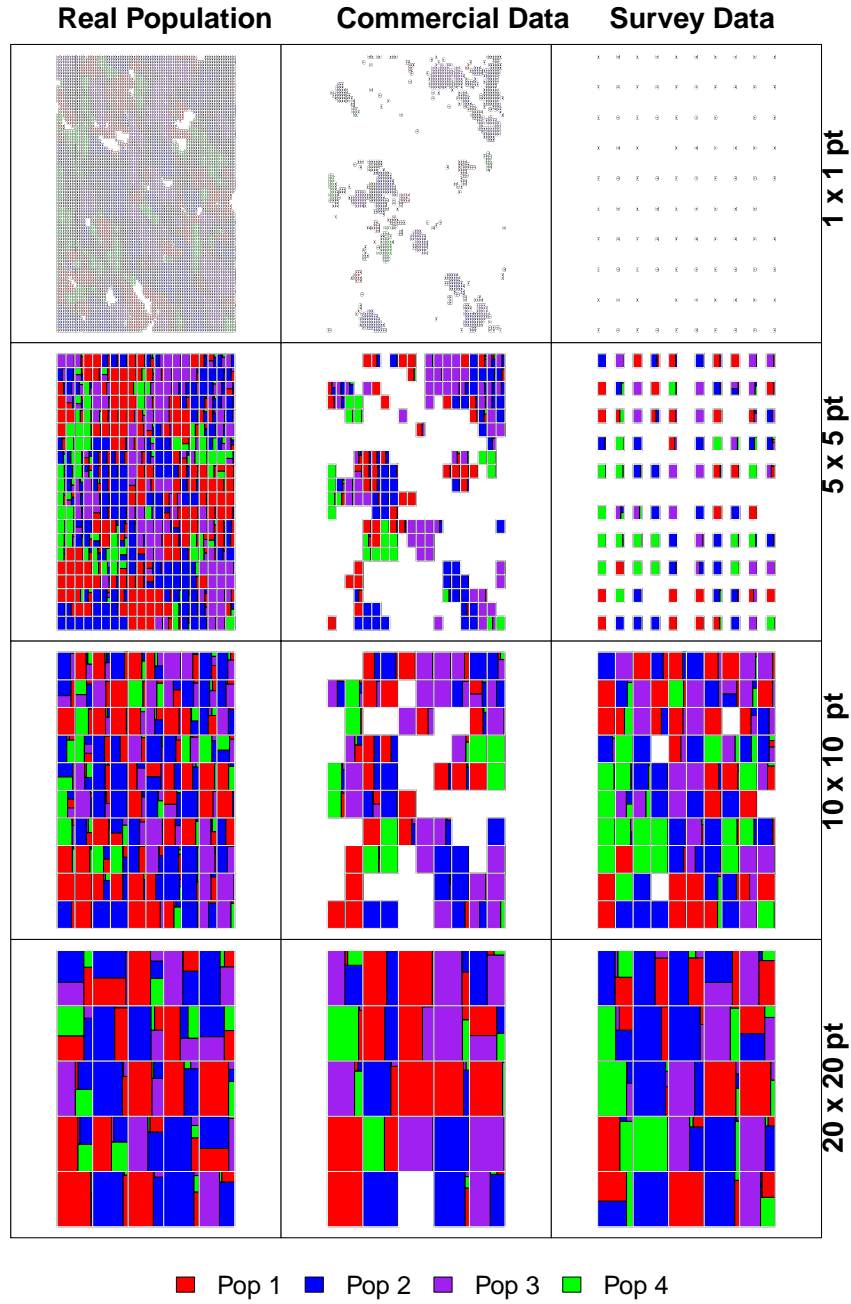


Figure 2: Data aggregation at different spatial resolutions over a ten year period

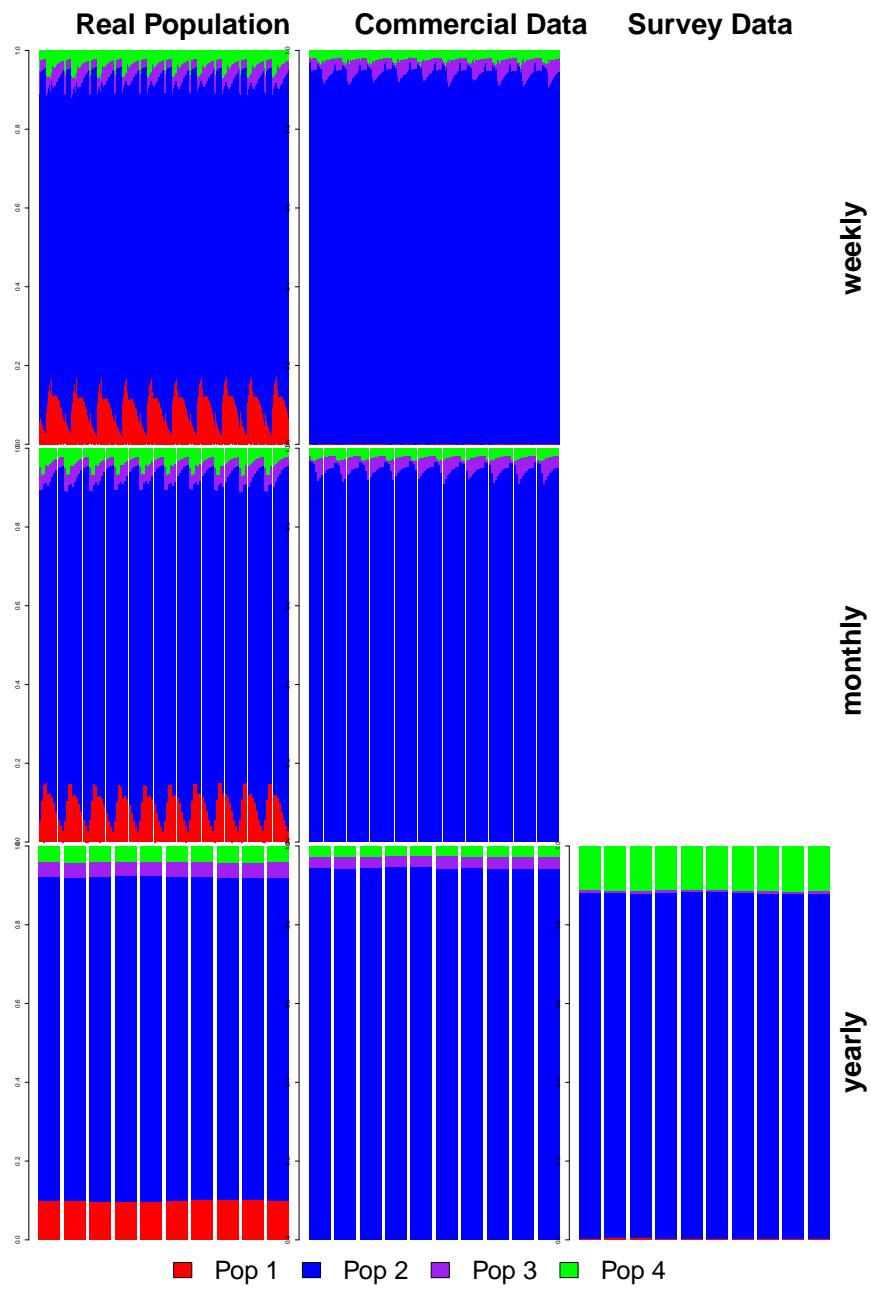


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

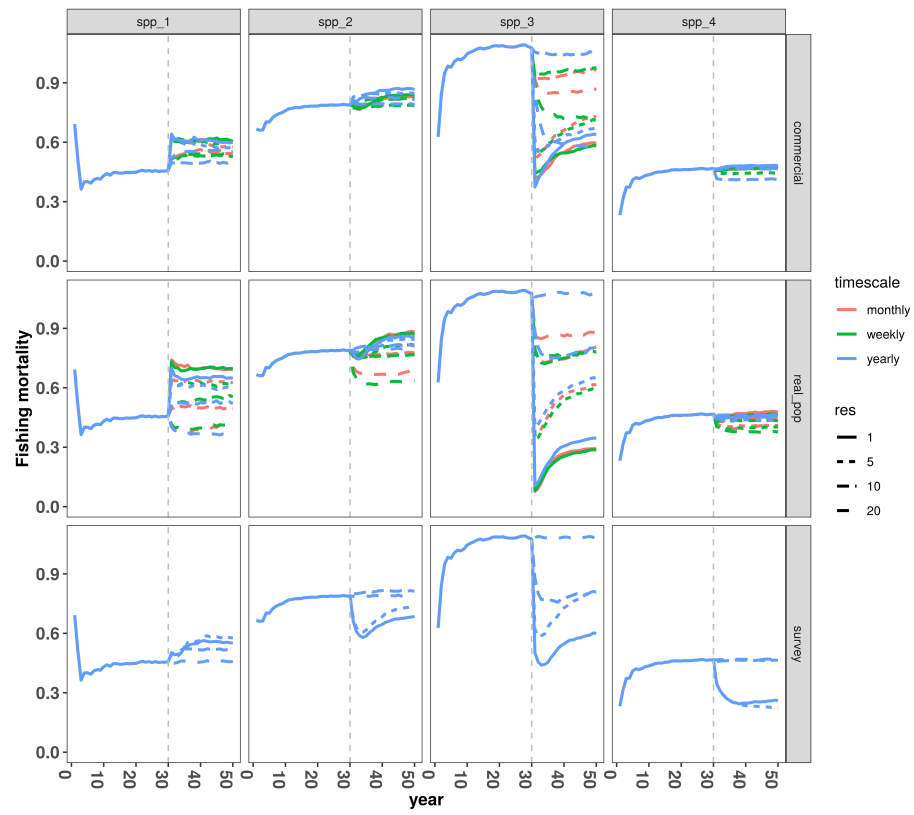


Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

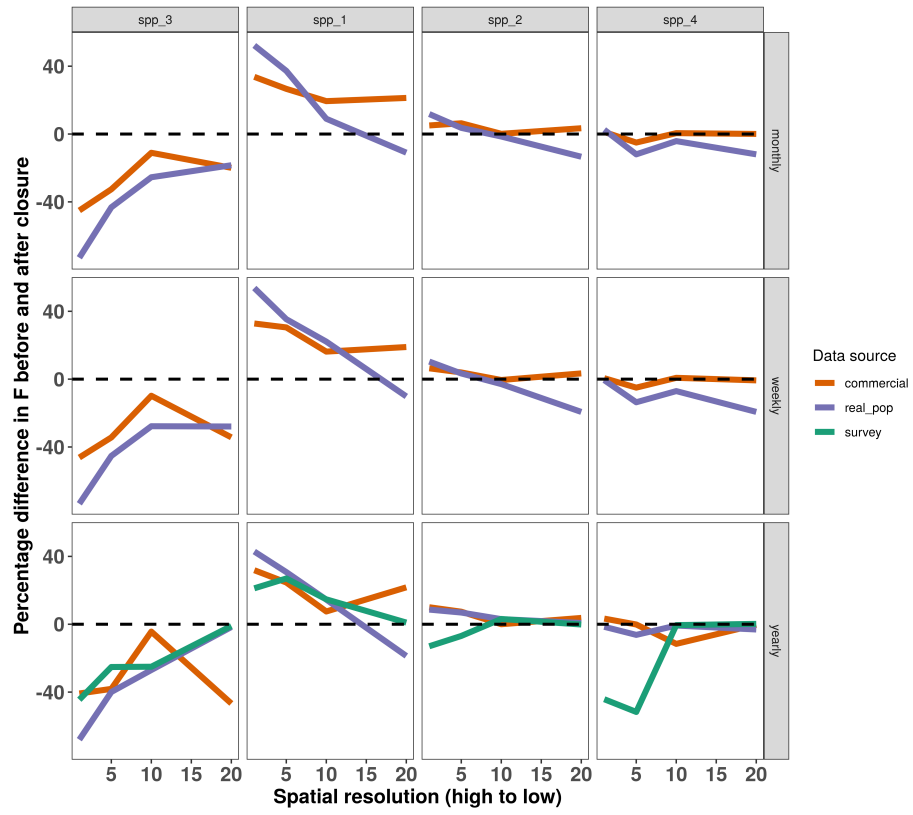


Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

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