

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

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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 developed a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement

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

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

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## 1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time, with varying knowledge of species distributions. 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

6 quota. This may lead to overexploitation of fish populations (Ulrich et al.,  
7 2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the abil-  
8 ity to maintain fishing mortality within sustainable limits (Alverson et al., 1994;  
9 Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the  
10 biological and economic sustainability of fisheries. As such, there is increasing  
11 interest in technical solutions such as gear and spatial closures as measures to  
12 reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill,  
13 2008; Bellido et al., 2011; Cosgrove et al., 2019).

14  
15 Adaptive spatial management strategies have been proposed as a way of  
16 reducing discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014).  
17 Implementation of avoidance measures is, however, restricted by lack of knowl-  
18 edge of fish and fishery spatiotemporal dynamics and understanding of the scale  
19 at which processes become important for management. Understanding the cor-  
20 rect scale for spatial measures is crucial for implementing solutions at a reso-  
21 lution that ensures effective management (Dunn et al., 2016) while minimising  
22 economic impact. For example, the problem can be to identify a scale that  
23 promotes species avoidance for vulnerable or low quota species while allowing  
24 continuance of sustainable fisheries for available quota species.

25  
26 Identifying appropriate spatial scales for fisheries closures has been a chal-  
27 lenge in the past but identified as crucial to its success (Costello et al., 2010;  
28 Dunn et al., 2016). Further, poorly sited closures have led to ineffectual mea-  
29 sures with unintended consequences. For example, increased benthic impact on  
30 previously unexploited areas was observed from the cod closure in the North Sea  
31 with a lack of observed intended effect in reducing cod exploitation (Rijnsdorp  
32 et al., 2001; Dinmore et al., 2003)). More refined spatiotemporal information  
33 has since become available through the combination of logbook and Vessel Mon-  
34 itoring System (VMS) data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen  
35 et al., 2012; Mateo et al., 2016) and more real-time spatial management has  
36 been possible (e.g. Holmes et al., 2011). Such information is, however, derived

37 from an inherently biased sampling programme, targeted fishing, where fishers  
38 establish favoured fishing grounds through an explore-exploit strategy (Bailey  
39 et al., 2018) where they search for areas with high catches and then use experi-  
40 ence to return to areas where they’ve experienced high catch in the past.

41

42 In order to understand the effect of spatiotemporal aggregation of data we  
43 ask two fundamental questions regarding inference derived from observational  
44 data:

- 45 1. How does sampling-derived data reflects the underlying community struc-  
46 ture?
- 47 2. How does data aggregation and source impact on spatial fisheries man-  
48 agement measures?

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

62

## 63 2. Materials and Methods

64 A simulation model that is modular and discrete-event based was developed.  
65 This approach enables efficient computation by allowing for sub-modules imple-  
66 mented on time-scales appropriate to capture the characteristic of the different  
67 processes (Figure 1). The following sub-modules were included to capture the  
68 full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population  
69 movement, 4) fishery dynamics.

70  
71 Population dynamics (fishing and natural mortality which are instantaneous  
72 rates, growth of the population biomass) operate on a daily time-step, while  
73 population movement occurs on a weekly time-step. Recruitment takes place  
74 periodically each year for a set time duration specified for each population, while  
75 the fishing module operates on a tow-by-tow basis (i.e. multiple events a day).

76 Population movement is a combination of random (diffusive) movement,  
77 governed by a stochastic process where movement between adjacent cells is  
78 described by a set of probabilities, and directed (advective) movement where  
79 at certain times of year the population moves towards spawning grounds by  
80 increasing the probabilities of moving into the spawning grounds from adjacent  
81 cells. We incorporate characterisation of a number of different fishing fleet dy-  
82 namics exploiting four fish populations with different spatial and population  
83 demographics. The following describes the implementation of each of the sub-  
84 modules.

### 85 2.1. Population dynamics

86 The basic population level processes were simulated using a modified two-  
87 stage Deriso-Schnute delay difference model which models the fish populations in  
88 terms of aggregate biomass of recruits and mature components rather than keep-  
89 ing track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A  
90 daily time-step was chosen to discretise continuous population processes on a bi-  
91 ologically relevant and computationally tractable timescale. Population biomass

growth and depletion for pre-recruits and recruited fish were modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment functionally linked to the adult population size. Biomass for each cell  $c$  was incremented each day  $d$  as follows (the full parameter list is detailed in Table 1):

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

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

102

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

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

where  $C_{c,d}$  is the summed catch from the fishing model across all fleets and vessels in cell  $c$  for the population during the day  $d$ , and  $B_{c,d}$  the daily biomass for the population in the cell. Here, catch 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.

114

## 115 2.2. Recruitment dynamics

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

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

119 Where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB)  
 120 required to produce half the maximum stock size,  $S$  current stock size and  $\sigma^2$   
 121 the variability in the recruitment due to stochastic processes, or a stochastic  
 122 Ricker form (Ricker, 1954):

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

123 where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density dependent  
 124 reduction in productivity as the SSB increases. In our example application the  
 125 Beverton-Holt form of stock recruit relationship was used for all populations  
 126 though either functional form can be chosen.

## 127 2.3. Population movement dynamics

128 To simulate fish population distribution in space and time a Gaussian spatial  
 129 process was employed to model habitat suitability for each of the populations  
 130 on a 2d grid. JM: MENTION IN THE INTRODUCTION

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

parameters to implement different spatial structures for the populations.

139

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  $J$ ,  $\lambda$  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).

153

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

JM: WHAT ABOUT INDIVIDUAL INTERACTIONS:w

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

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



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

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

## 2.4. Fleet dynamics

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

### 2.4.1. Fleet targeting

Each fleet of  $n$  vessels was characterised by both a general efficiency,  $Q_{fl}$ , and a population specific efficiency,  $Q_{fl,p}$ . Thus, the product of these parameters  $[Q_{fl} \cdot Q_{fl,p}]$  affects the overall catch rates for the fleet and the preferential targeting of one population over another. This, in combination with the param-

194 eter choice for the step-function defined below (as well as some randomness from  
195 the exploratory fishing process) determined the preference of fishing locations  
196 for the fleet. All species prices were kept the same across fleets and seasons.

#### 197 *2.4.2. Trip-level decisions*

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

#### 208 *2.4.3. Within-trip decisions*

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

222

223 We use a *Lévy flight* which is a particular form of random walk charac-  
 224 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-  
 225 ceived a lot of attention in ecological theory in recent years as having shown to  
 226 have very similar characteristics as those observed by animals in nature, and  
 227 being a near optimum searching strategy for predators pursuing patchily dis-  
 228 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,  
 229 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a  
 230 stochastic search pattern similar to that observed with a lévy flight. However,  
 231 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),  
 232 with the contention that search patterns may be more simply characterised as  
 233 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the  
 234 characteristics of the prey field (Sims et al., 2012).

235  
 236 For our implementation of a random walk directional change is based on  
 237 a negatively correlated circular distribution where a favourable fishing ground  
 238 is likely to be “fished back over” by the vessel returning in the direction it  
 239 came from. The step length (i.e. the distance travelled from the current to the  
 240 next fishing location) is determined by recent fishing success, measured as the  
 241 summed value of fish caught (revenue,  $Rev$ ),

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

242 where  $L_p$  is landings of a population  $p$ , and  $Pr_p$  price of a population. Here,  
 243 when fishing is successful vessels remain in a similar location and continue to  
 244 exploit the local fishing grounds. When unsuccessful, they move some distance  
 245 away from the current fishing location. The movement distance retains some  
 246 degree of stochasticity, that can be controlled separately, but is determined by  
 247 the relationship:

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

248 Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function

249 in its relation to revenue, so that, a step from  $(x1, y1)$  to  $(x2, y2)$  is defined by:

$$\begin{aligned}
 (x2, y2) = & x1 + StepL \cdot \cos\left(\frac{\pi \cdot Br}{180}\right), \\
 & y1 + StepL \cdot \sin\left(\frac{\pi \cdot Br}{180}\right) \\
 \text{with } & Br_{t-1} < 180, Br_t = 180 + \sim vm[(0, 360), k] \\
 & Br_{t-1} > 180, Br_t = 180 - \sim vm[(0, 360), k]
 \end{aligned} \tag{9}$$

250 where  $k$  the concentration parameter from the von Mises distribution that we  
 251 correlate with the revenue so that  $k = (Rev + 1/RefRev) * max_k$ , where  $max_k$   
 252 is the maximum concentration value,  $k$ , and  $RefRev$  is parametrised as for  $\beta_3$   
 253 in the step length function. A realised example of the step length and turning  
 254 angle relationships to revenue can be seen at Figure S12.

#### 255 2.4.4. Local population depletion

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

#### 267 2.5. Fisheries independent survey

268 A fisheries-independent survey is simulated where fishing on a regular grid  
 269 begins each year at the same time for a given number of stations (a fixed station  
 270 survey design). Catches of the populations at each station are recorded but not  
 271 removed from the population (catches are assumed to have negligible impact  
 272 on population dynamics). This provides a fishery independent snapshot of the

273 populations at a regular spatial intervals each year, similar to scientific surveys  
274 undertaken by fisheries research agencies.

275

## 276 *2.6. Software: R-package development*

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

280

## 281 **3. Parameterisation**

### 282 *3.1. Population models*

283 We parametrised the simulation model for four populations with different  
284 demographics; growth rates, natural mortality and recruitment functions (Ta-  
285 ble 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3,  
286 S4) were defined to be unique to each population resulting in differently weekly  
287 distribution patterns (Figures S5-S7). In addition, each of the populations was  
288 assumed to have two defined spawning areas that result in the populations mov-  
289 ing towards these areas in pre-defined weeks (Figure S2) with population-specific  
290 movement rates (Table 4). In such a configuration, the individual habitat pref-  
291 erences and thermal tolerances result in different spatial habitat use for each  
292 population (Figure 2) and consequently different seasonal exploitation patterns  
293 (Fishing mortality in Figure 3).

### 294 *3.2. Fleet parametrisation*

295 The fleets were parametrised to reflect five different characteristic fisheries  
296 with unique exploitation dynamics (Table 5). By setting different catchability  
297 parameters ( $Q_{fl,p}$ ) we create different targeting preferences between the fleets  
298 and hence spatial dynamics. The random walk process implies that within a  
299 fleet different vessels have different spatial distributions based on individual

300 experience. The step function was parametrised dynamically within the simu-  
 301 lations as the maximum revenue obtainable was not known beforehand. This  
 302 was implemented so that vessels take smaller steps when fishing at a location  
 303 that yields landings value in the top 90th percentile of the value experienced in  
 304 that year so far (as defined per fleet in Table 5).

305

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

315

### 316 3.3. *Survey settings*

317 The survey simulation was set up with a fixed gridded station design with  
 318 100 stations fished each year, starting on day 92 and ending on day 112 (5  
 319 stations per day) with same catchability parameters for all populations ( $Q_p =$   
 320 1). This approximates a real world survey design with limited seasonal and  
 321 spatial coverage.

### 322 3.4. *Example research question*

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

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

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

334  
335 The following steps are undertaken to determine closures:

- 336 1. Extract data source
- 337 2. Aggregate according to desired spatial and temporal resolution
- 338 3. Interpolate across entire area at desired resolution using simple bivariate  
339 kriging using the *interp* function from the R package *akima* (Akima, 2006).  
340 This is intended to represent a naive spatial model of catch rates, without  
341 knowledge of the spatial population dynamics.
- 342 4. Close area covering top 5 % of catch rates

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

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

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

## 350 4. Results

### 351 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 S9),

while across several trips fishing grounds that are further apart are fished (Figure S10). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 4, where several trips for the vessel overlaid on the revenue field, i.e.

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

Vessels from the same fleet (and therefore targeting preference) may exploit some shared and some different fishing grounds depending on their own personal experience during the explore phase of the fishery (Figure S11). This results from the randomness in the correlated random walk step function, with distance moved during the exploitation phase and the direction stochastically related to the revenue experienced on the fishing ground (Figure S12).

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

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

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

Figure 5 shows the aggregated catch composition from each of the data sources over a ten-year period (to average seasonal patterns) at different spatial resolutions. The finer spatial grid for the real population (top left) and commercial data (top middle) show visually similar patterns, though there are large unsampled areas in the commercial data from a lack of fishing activity (particularly in the lower left part of the sampling domain). The survey data at this spatial resolution displays very sparse information about the spatial distributions of the populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns and, while losing some of the spatial detail, there remains good



375 consistency between the 'real population' and the commercial data. Survey data  
376 starts to pick out some of the similar patterns as the other data sources, but  
377 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and  
378 20 x 20 grid lose a significant amount of information about the spatial resolu-  
379 tions for all data sources, and some differences between the survey, commercial  
380 and 'real population' data emerge.

381

382 Figure 6 shows the consequences of different temporal aggregations of the  
383 data over a ten-year period, with weekly (top), monthly (middle) and yearly  
384 (bottom) catch compositions from across an aggregated 20 x 20 area. By com-  
385 parison to the 'real population', the monthly aggregation captures the major  
386 patterns seen in the weekly data, albeit missing more subtle differences. The  
387 yearly data assumes the same proportion of each population caught at any time  
388 of the year due to the data aggregation. This assumption introduces 'aggrega-  
389 tion bias' as the data may only be representative of some point (or no point) in  
390 time. The commercial data on a weekly basis shows some of the same patterns  
391 as the 'real population', though the first species (in red) is less well represented  
392 and some weeks are missing catches from the area. The monthly data shows  
393 some consistency between the 'real population' and commercial data for species  
394 2 - 4, though species 1 remains under-represented. On an annual basis, inter-  
395 estingly the commercial data under represents the first species (in red) while  
396 the survey over represents species 1. This is likely due to the biases in com-  
397 mercial sampling, with the fisheries not targeting the areas where species 1 are  
398 present and the survey sampling areas where species 1 is more abundant than  
399 on average.

#### 400 *4.3. How does data aggregation and source impact on spatial fisheries manage-* 401 *ment measures?*

402 We implemented a spatial closure using the different data sources and spatial  
403 and temporal aggregations as outlined in the protocol in Section 3.4. We used  
404 this to assess the efficacy of a closure in reducing fishing mortality on species 3,

405 given availability of data and its use at different resolutions in order to evaluate  
406 the trade-offs in data sources.

407 The trend in fishing mortality for each species show that in most cases the  
408 fishery closure was successful in reducing fishing mortality on the species of in-  
409 terest (species 3; Figure 7), though interestingly the largest reductions in fishing  
410 mortality happened immediately after the closures, following which the fisheries  
411 "adapted" to the closures and fishing mortality increased again somewhat. The  
412 exception to the success was the closures implemented based on the coarsest  
413 spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all  
414 data sources. As expected, closures based on the "known" population distribu-  
415 tion were most effective, with differing degrees of success using the commercial  
416 data. Fishing mortality rates on the other species changed in different propor-  
417 tions, depending on whether the displaced fishing effort moved to areas where  
418 the populations were found in greater or lesser density.

419  
420 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))  
421 highlights that the factor most contributing to differences in fishing mortality  
422 before and after the closure was the population (72 % showing that the closures  
423 were effective for population 3), followed by data resolution (21 %), data type  
424 (7 %) with the least important factor the timescale (< 1 %). In general the finer  
425 the spatial resolution of the data used the greater reduction in fishing mortality  
426 for population 3 after the closures (Figure 8). The notable outliers are the com-  
427 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly  
428 timescale, where closures were nearly as effective as the fine-scale resolution. In  
429 this case the closures were sufficiently large to protect a core area of the habitat  
430 for the population, but this was achieved in a fairly crude manner by closing a  
431 large area - including area where the species was not found (Figure 9) that may  
432 have consequences in terms of restricting the fishery in a much larger area than  
433 necessary.

434

## 435 5. Discussion

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

### 454 5.1. *Simulation dynamics*

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

460  
461 Our approach is unique in that it captures fine scale population and fish-  
462 ery dynamics and their interaction in a way not usually possible with real data  
463 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

494 that understanding of the community composition dynamics will depend on the  
495 level of data aggregation and its important to consider the scale of processes;  
496 including population movement rates, habitat uniformity and fishing targeting  
497 practices if potential biases in data are to be understood and taken into account.

498

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

510

### 511 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 512 *ment measures?*

513 From our simulations spatial disaggregation was more important than the  
514 temporal disaggregation of the commercial data. This reflects the fact that there  
515 was greater spatial heterogeneity over the spatial domain than experienced in  
516 individual locations over the course of the year (Figure 2). This indicates that  
517 fixed closures, at the right resolution, when based on commercially derived data  
518 have the potential to reduced fishing mortality. The likely cost of poor spatial  
519 and temporal resolution is associated with reduced effectiveness and potentially  
520 closing fishing opportunities for other fisheries.

521

522 Two contrasting real world approaches in this respect were the spatial clo-  
523 sures 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.

#### 5.4. Model assumptions and caveats

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

Fish populations in our simulations move in pre-defined timescales and according to fixed habitat preferences and temperature gradients (Figures S1, S3). Our assumptions in parametrising the model (movement rates, temperature tolerances) will have a direct impact on our conclusions on the relative importance of spatial and temporal processes. These assumptions could be explored in a future study by varying the parameters and assessing the robustness of our conclusions. For our example application we have chosen movement rates to reflect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

In addition, we have assumed that fishing vessels are not restricted by quota and therefore discarding of species for which vessels have no quota or that are

554 unwanted is not taken into account. This is likely to be a significant source of  
 555 bias in any inference using commercial data and should also be explored. For  
 556 example, MixFishSim could be altered to allow for spatiotemporal appraisal of  
 557 the impact of discarding on fisher behaviour and underlying populations via in-  
 558 clusion as discarding behaviour, or through move-on rules or cessation of fishing  
 559 activity when quota is exhausted.

560

### 561 *5.5. Future applications of MixFishSim*

562 We consider that the increased availability of high resolution catch and lo-  
 563 cational information from commercial fisheries will require it to be a key source  
 564 of data for ensuring management is implemented at the right scale in future.  
 565 For example, identifying hot-spots for bycatch reduction or identifying spatial  
 566 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,  
 567 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the  
 568 potential to test some of the assumptions behind the modelling approaches in  
 569 identifying such hotspots and indeed behind spatiotemporal modelling in gen-  
 570 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-  
 571 els under different data generation processes as exemplified by Stock et al. (2019)).

572

573 Other novel applications of our framework could be; testing different sur-  
 574 vey designs given multiple species and data generating assumptions (Xu et al.,  
 575 2015); commercial index standardisation methods and approaches and under-  
 576 standing of appropriate scales and data aggregations and non-proportionality  
 577 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);  
 578 exploring assumptions about the distribution of natural mortality and fishing  
 579 mortality throughout the year and importance of capturing in-year dynamics  
 580 in estimating stock status (Liu and Heino, 2013); at sea sampling scheme de-  
 581 signs to deliver unbiased estimates of population parameters Cotter and Pilling  
 582 (2007); Kimura and Somerton (2006); adaptive management (Walters, 2007;  
 583 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



613 in designing any closure scenario based on observational sampling. This infor-  
614 mation can then be used to set the bounds on data aggregation used in modelling  
615 studies aimed at informing the management measures.

616

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

## 625 **Abbreviations**

626 Detail any unusual ones used.

## 627 **Acknowledgements**

628 those providing help during the research..

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631 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn  
632 program (DP227AC).

## 633 **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 $d$	$d^{-1}$
$S_{c,d}$	is the stock size in cell $c$ for day $d$	$d^{-1}$
$\alpha$	the maximum recruitment rate	kg
$\beta$	the stock size 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

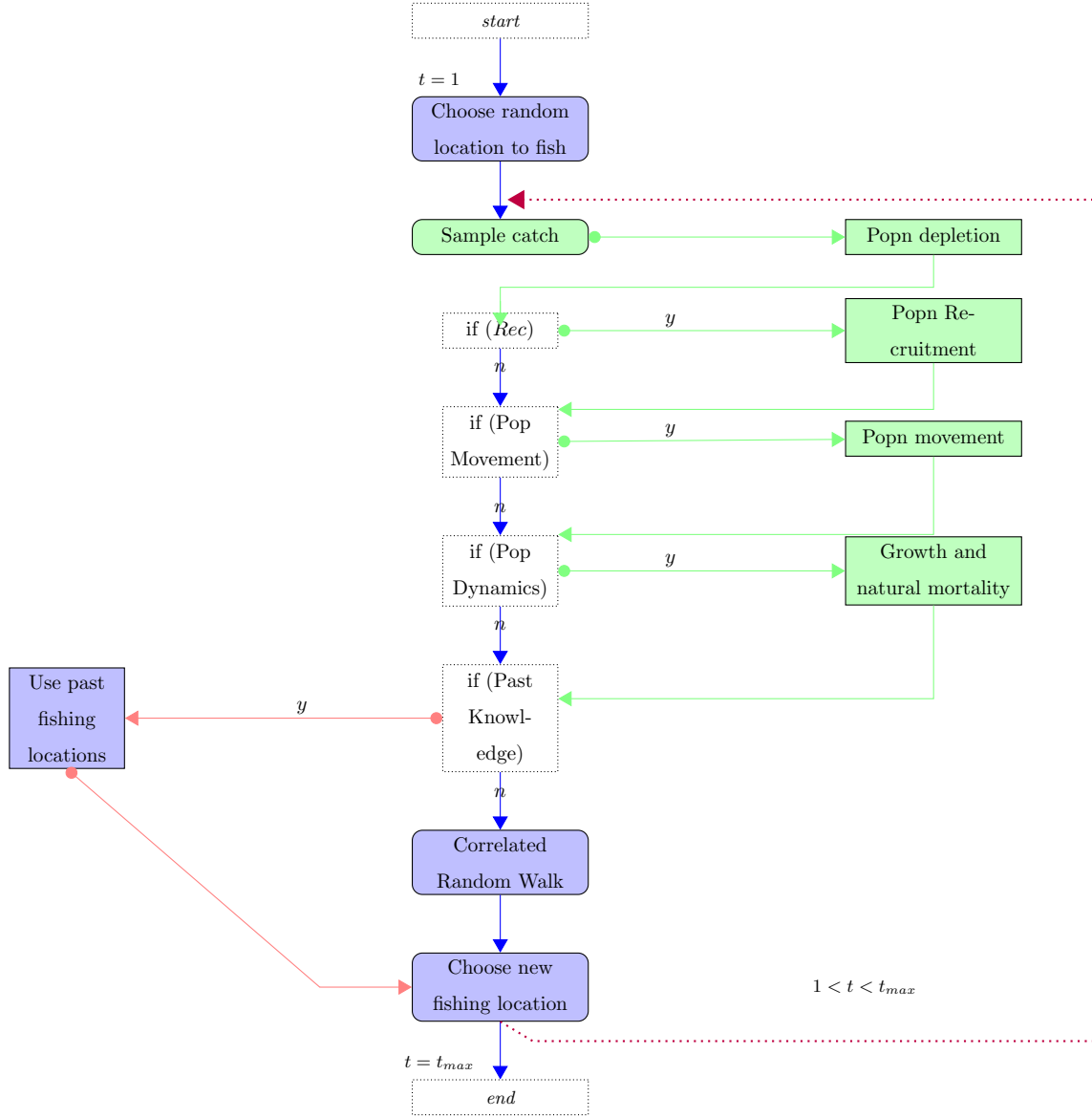


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur;  $t = \text{tow}$ ,  $t_{max}$  is the total number of tows; (Rec), (Pop Movement), (Pop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



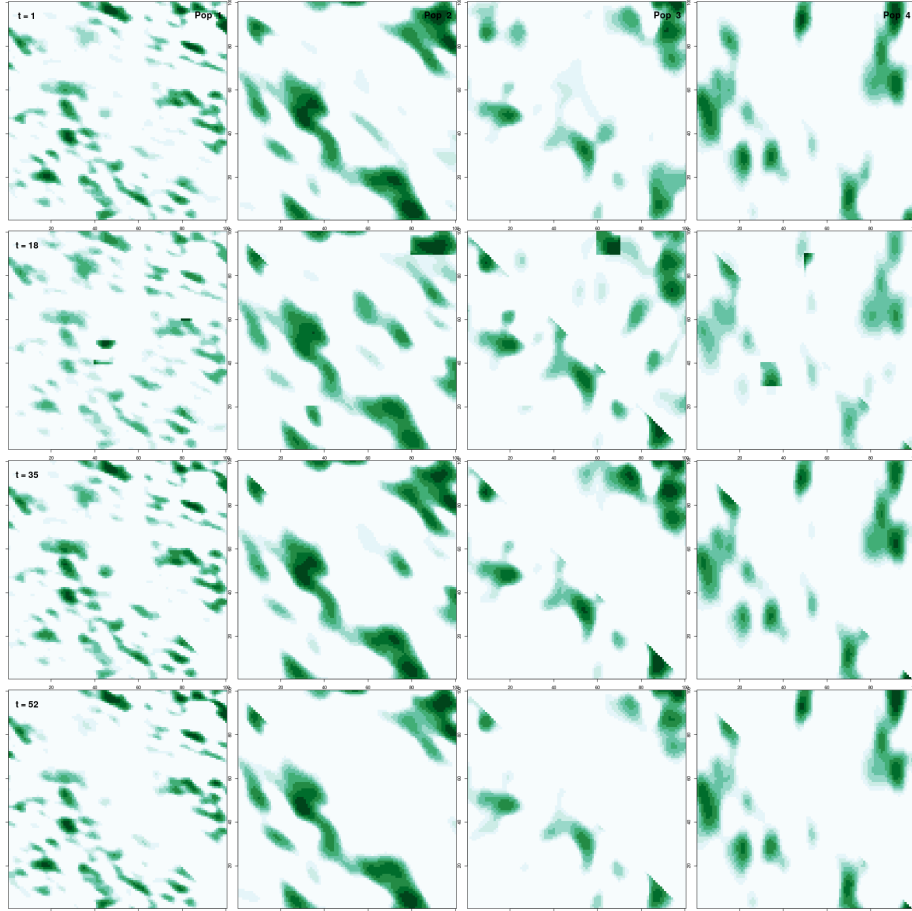


Figure 2: Simulated spatial dynamics - the four populations abundance ( $\log+1$ ) at four time steps.

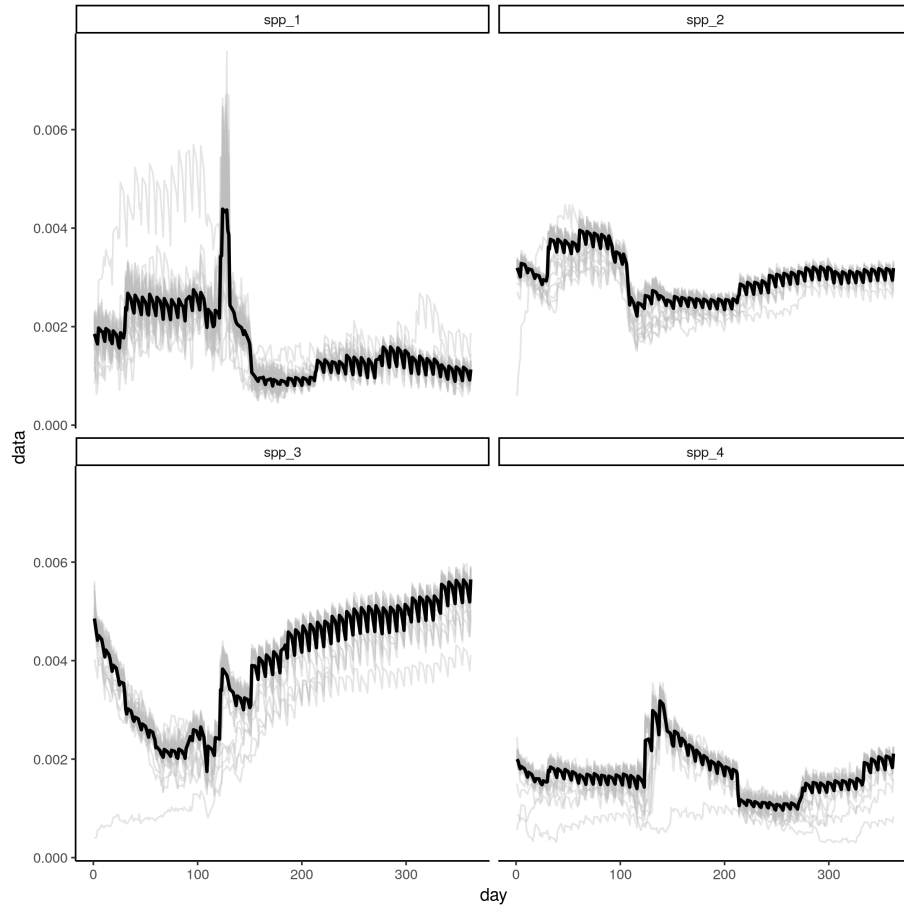


Figure 3: Fishing mortality dynamics - the daily fishing mortalities showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

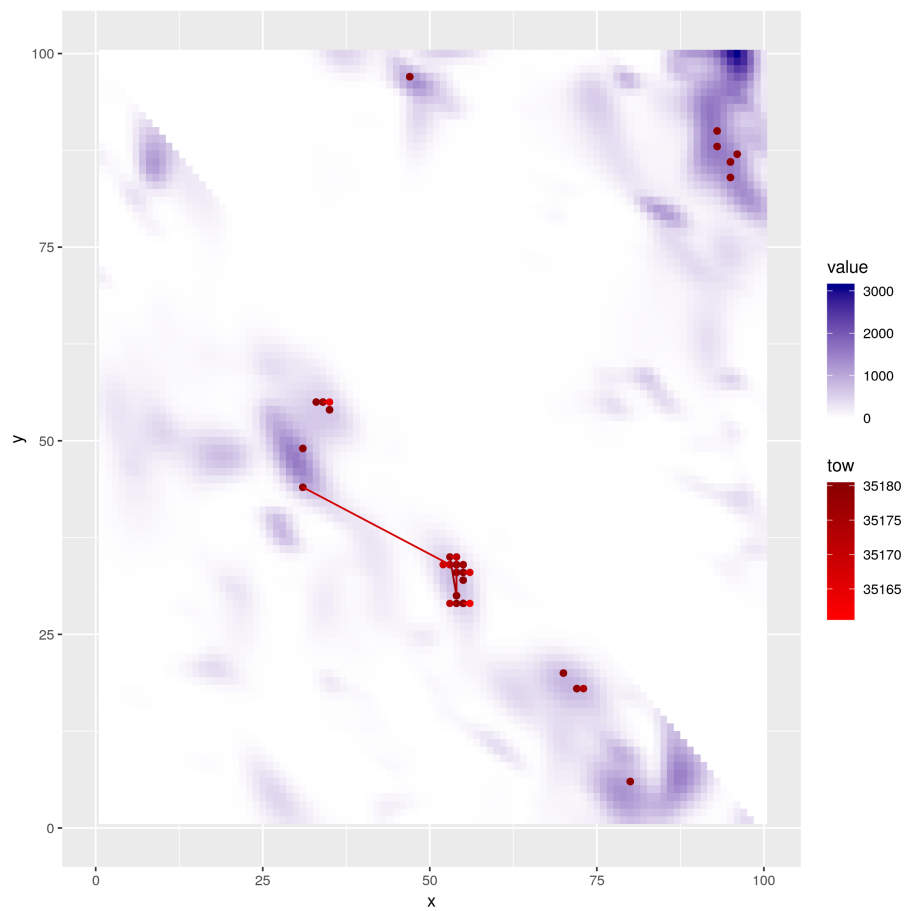


Figure 4: movement of a fleet over a single trip reference overlaid on the value field (i.e. sum of the population abundance  $\times$  catchability  $\times$  value

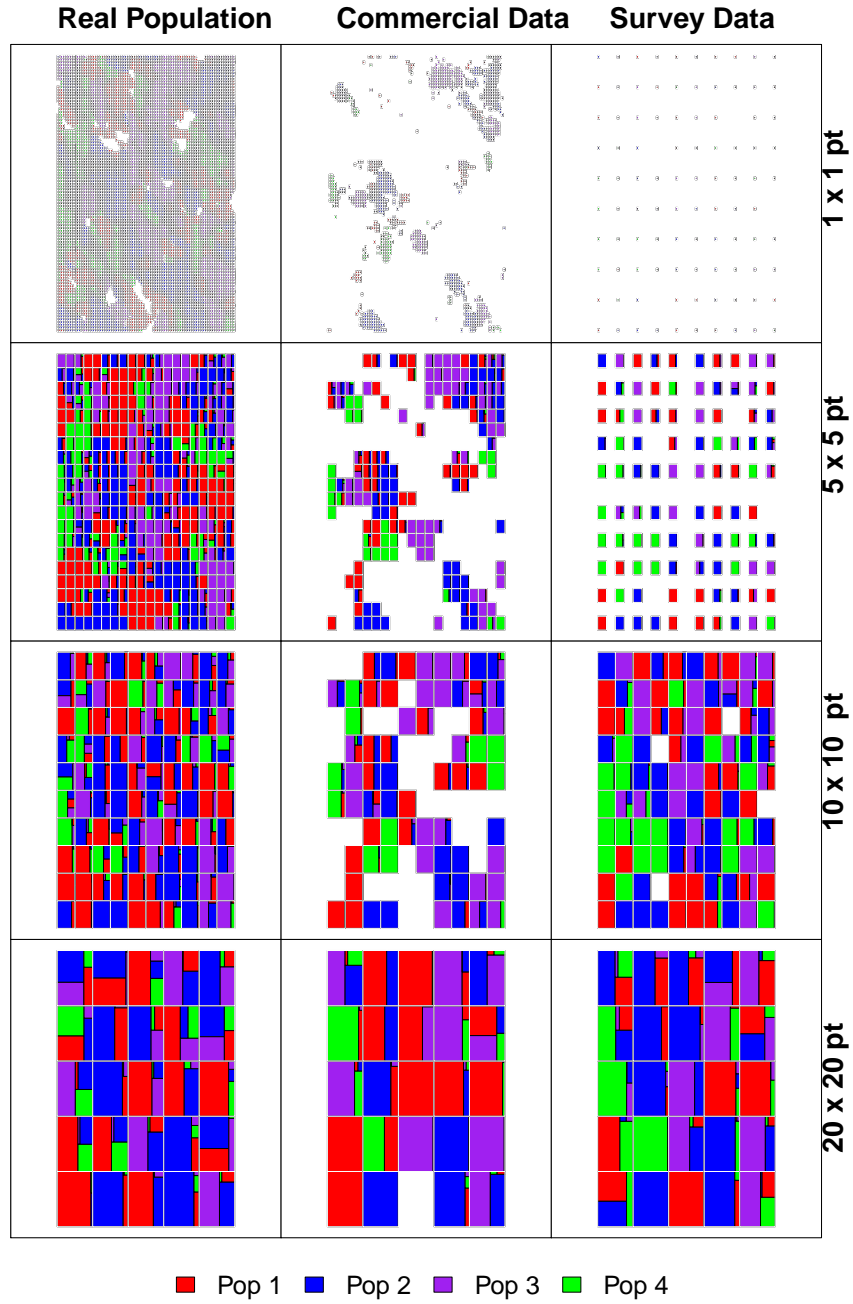


Figure 5: Data aggregation at different spatial resolutions over a ten year period

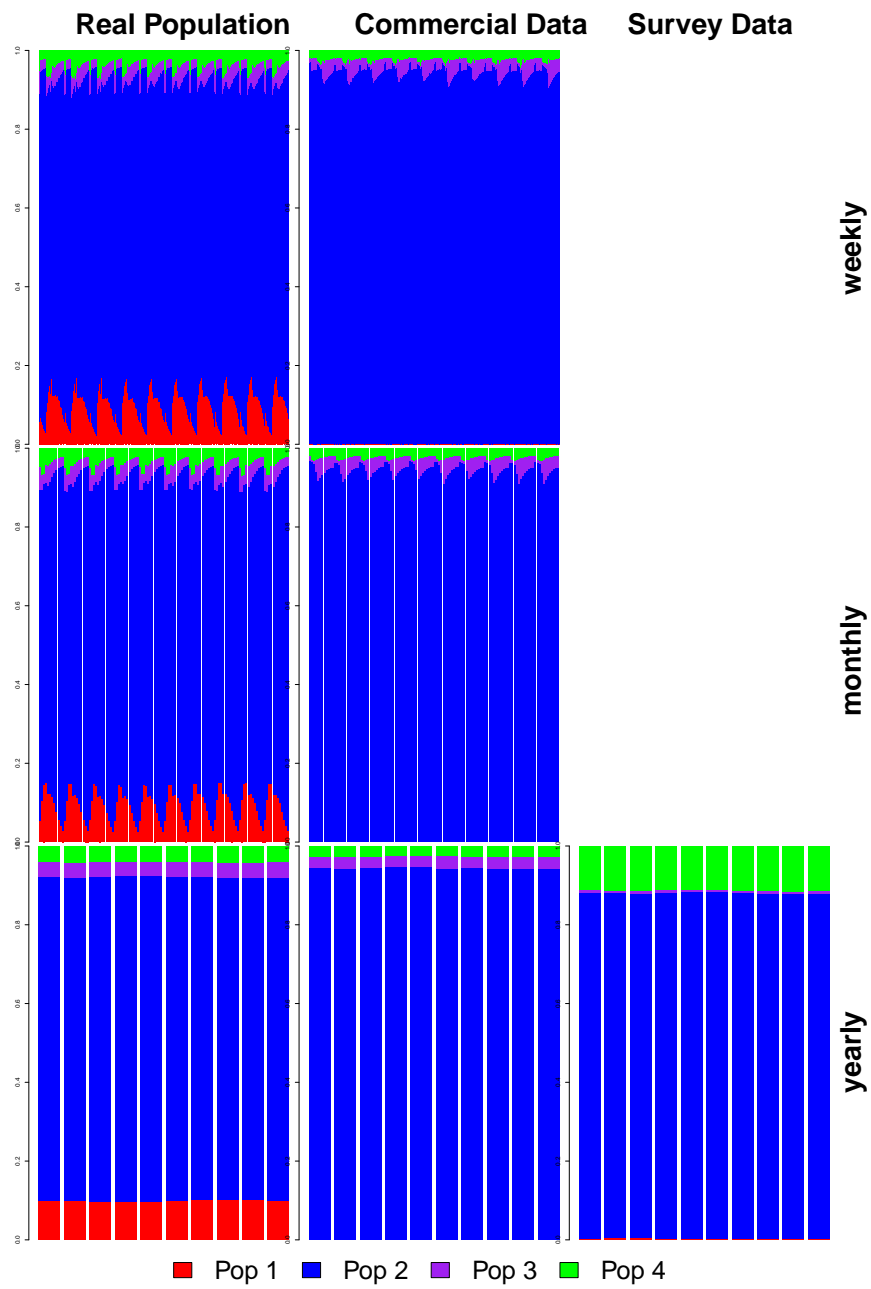


Figure 6: Data aggregation at different temporal resolutions over a ten-year period

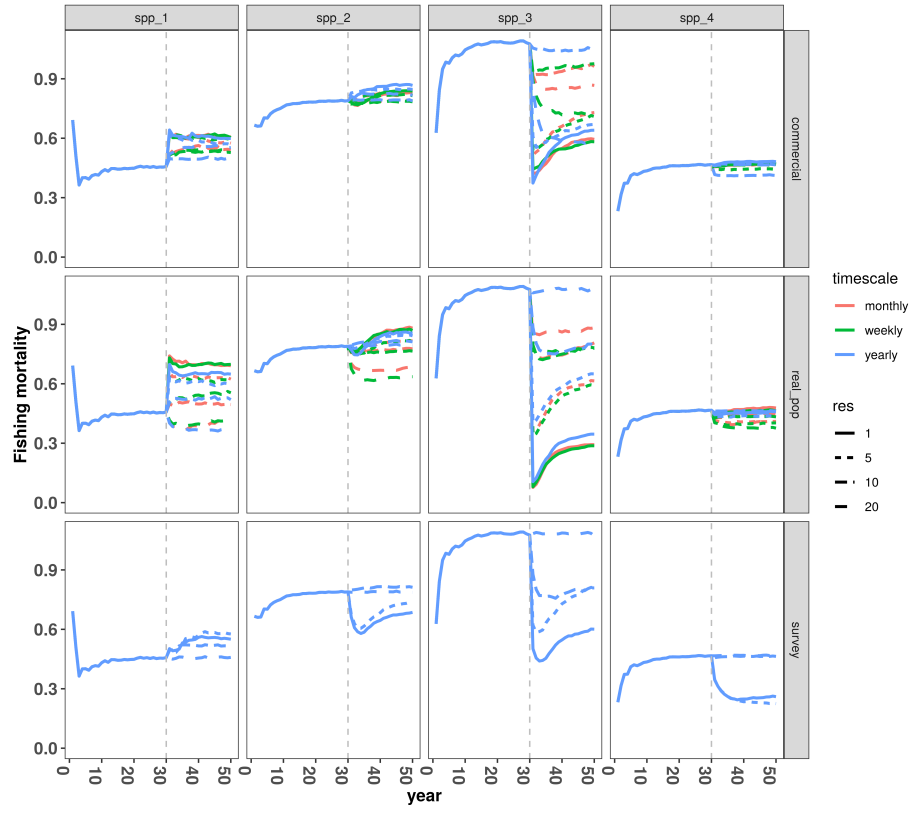


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

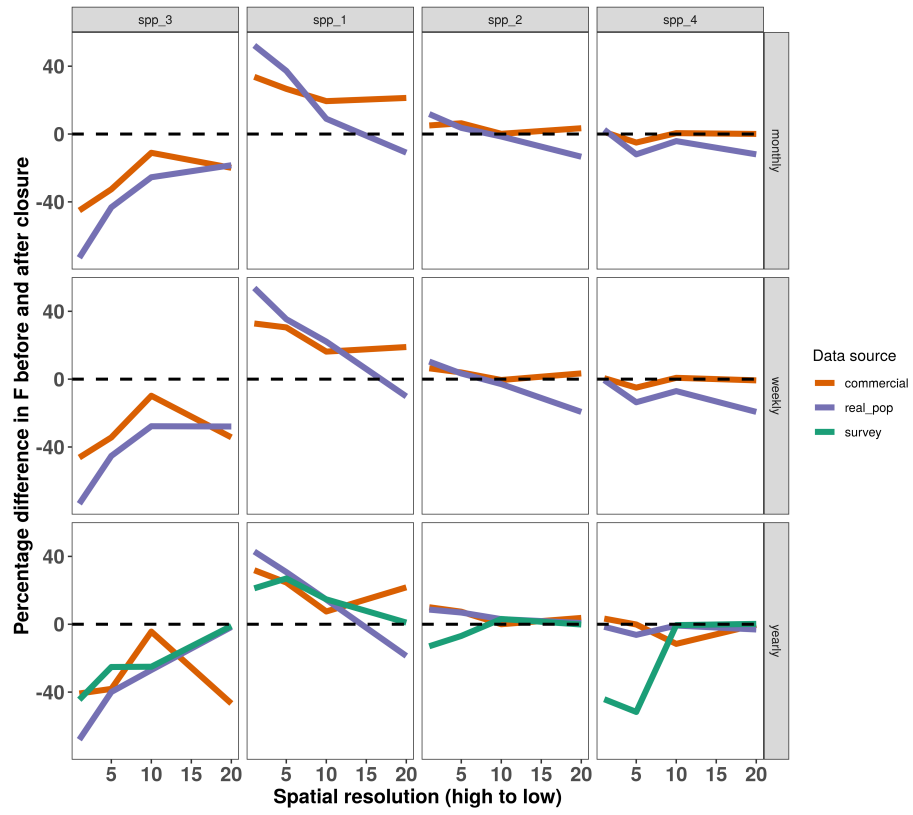


Figure 8: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

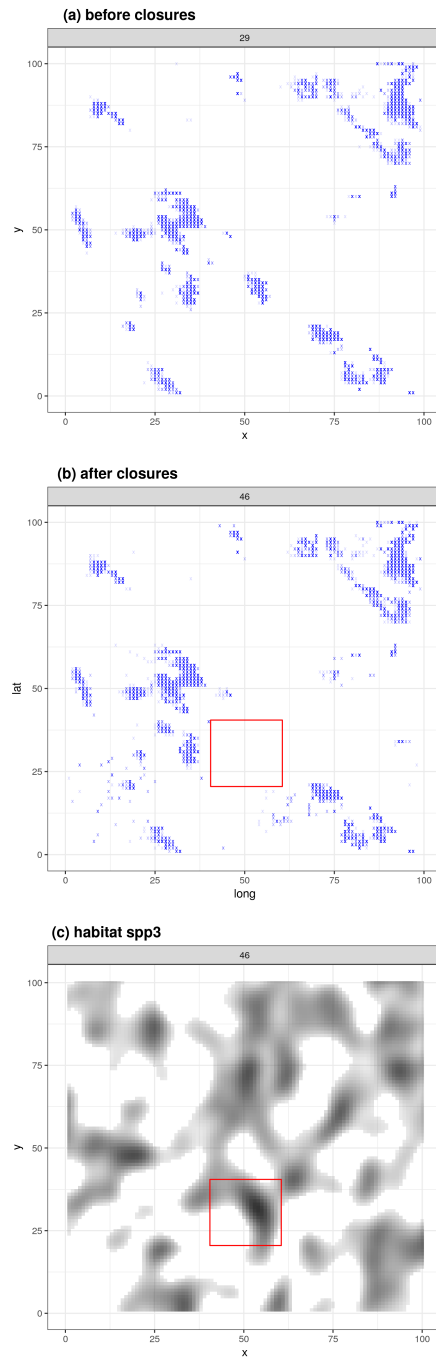


Figure 9: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) species 3 habitat distribution



## 634 References

- 635 Akima, H., 2006. Interpolation of irregularly spaced data, The akima Package. Interpolation  
636 of Irregularly and Regularly Spaced Data .
- 637 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of  
638 fisheries bycatch and discards.
- 639 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,  
640 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled  
641 human–environmental systems: the POSEIDON model of ocean fisheries.
- 642 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search  
643 Strategies: A Quantitative Random Walk Analysis. *Ecological Society of America* 86,  
644 3078–3087.
- 645 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping  
646 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel  
647 geo-location. *Fisheries Research* 106, 41–53.
- 648 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading  
649 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,  
650 715–736.
- 651 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards  
652 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*  
653 670, 317–333.
- 654 Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant move-  
655 ments of fishermen: The same foraging strategy as natural predators. *Ecological Applica-*  
656 *tions* 17, 331–337.
- 657 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 658 Catchpole, T.L., Revall, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*  
659 *Fish Biology and Fisheries* 18, 17–31.
- 660 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in  
661 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- 662 Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh,  
663 M., 2019. A game of two halves: Bycatch reduction in Nephrops mixed fisheries. *Fisheries*  
664 *Research* 210, 31–40.

Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A., 2010. The value of spatial information in MPA network design. *Proceedings of the National Academy of Sciences* .

Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys: Improving the protocols for sampling commercial fisheries. *Fish and Fisheries* 8, 123–152.

Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch: Implications for Management. *Fisheries* 23, 8–17.

Dedman, S., Officer, R., Brophy, D., Clarke, M., Reid, D.G., 2015. Modelling abundance hotspots for data-poor Irish Sea rays. *Ecological Modelling* 312, 77–90.

Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. [arXiv:1410.7455v3](#).

Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Application of a weekly delay-difference model to commercial catch and effort data for tiger prawns in Australia 's Northern Prawn Fishery. *Fisheries Research* 65, 335–350.

Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S., 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES Journal of Marine Science* 60, 371–380.

Dolder, P.J., Thorson, J.T., Minto, C., 2018. Spatial separation of catches in highly mixed fisheries. *Scientific Reports* .

Dunn, D.C., Boustany, A.M., Roberts, J.J., Brazer, E., Sanderson, M., Gardner, B., Halpin, P.N., 2014. Empirical move-on rules to inform fishing strategies: A New England case study. *Fish and Fisheries* 15, 359–375.

Dunn, D.C., Maxwell, S.M., Boustany, A.M., Halpin, P.N., 2016. Dynamic ocean management increases the efficiency and efficacy of fisheries management. *Proceedings of the National Academy of Sciences* , 201513626.

Edwards, A.M., Station, P.B., Canada, O., 2011. Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. *Ecology* 92, 1247–1257.

F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography* 30, 609–628.

698 Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne,  
699 P., Gorton, R., Gamble, R.J., Smith, A.D., Smith, D.C., 2011. Lessons in modelling and  
700 management of marine ecosystems: The Atlantis experience. *Fish and Fisheries* .

701 Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and temporal statistical  
702 analysis of bycatch data: patterns of sea turtle bycatch in the North Atlantic. *Canadian*  
703 *Journal of Fisheries and Aquatic Sciences* 65, 2461–2470.

704 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B.M., 2012. Spatial patterns in the re-  
705 tained catch composition of Irish demersal otter trawlers: High-resolution fisheries data as  
706 a management tool. *Fisheries Research* 129-130, 127–136.

707 Gillis, D.M., Peterman, R.M., 1998. Implications of interference among fishing vessels and  
708 the ideal free distribution to the interpretation of CPUE. *Canadian Journal of Fisheries*  
709 *and Aquatic Sciences* 55, 37–46.

710 Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A., Vermard, Y.,  
711 Marchal, P., 2016. Thirty years of fleet dynamics modelling using discrete-choice models:  
712 What have we learned? *Fish and Fisheries* , 1–18.

713 Girardin, R., Vermard, Y., Thébaud, O., Tidd, A., Marchal, P., 2015. Predicting fisher  
714 response to competition for space and resources in a mixed demersal fishery. *Ocean &*  
715 *Coastal Management* 106, 124–135.

716 Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional to abundance?  
717 *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760–1772.

718 Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice, dynamics and  
719 uncertainty. volume 2. [arXiv:1011.1669v3](https://arxiv.org/abs/1011.1669v3).

720 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,  
721 2011. Using fishery-dependent data to inform the development and operation of a co-  
722 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*  
723 *Science* 68, 1679–1688.

724 Hutton, T., Mardle, S., Pascoe, S., Clark, R.a., 2004. Modelling fishing location choice within  
725 mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Journal of Marine*  
726 *Science* 61, 1443–1452.

727 Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the philosophy of fishing  
728 technology. *Fish and Fisheries* 3, 340–355.

729 Kimura, D.K., Somerton, D.A., 2006. Review of statistical aspects of survey sampling for  
730 marine fisheries. *Reviews in Fisheries Science* 14, 245–283.

731 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and accessible meth-  
732 ods to provide high-resolution estimates of fishing-effort distributions from vessel monitor-  
733 ing system (VMS) data. *ICES Journal of Marine Science* 67, 1260–1271.

734 Little, A.S., Needle, C.L., Hilborn, R., Holland, D.S., Marshall, C.T., 2014. Real-time spatial  
735 management approaches to reduce bycatch and discards: experiences from Europe and the  
736 United States. *Fish and Fisheries* , n/a–n/a.

737 Liu, X., Heino, M., 2013. Overlooked biological and economic implications of within-season  
738 fishery dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* .

739 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for  
740 evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling*  
741 .

742 Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fisheries. *ICES*  
743 *Journal of Marine Science* .

744 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species distribution  
745 modeling: a statistical review with focus in spatio-temporal issues.

746 Mateo, M., Pawlowski, L., Robert, M., 2016. Highly mixed fisheries: fine-scale spatial patterns  
747 in retained catches of French fisheries in the Celtic Sea. *ICES Journal of Marine Science:*  
748 *Journal du Conseil* , fsw129.

749 Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: A review of recent  
750 approaches. *Fisheries Research* .

751 Needle, C.L., Catarino, R., 2011. Evaluating the effect of real-time closures on cod targeting.  
752 *ICES Journal of Marine Science* 68, 1647–1655.

753 Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D.,  
754 Thorson, J.T., Fulton, E.A., Smith, A.D.M., Smith, F., Bayliss, P., Haywood, M., Lyne,  
755 V., Rothlisberg, P.C., 2014. Multispecies fisheries management and conservation: tactical  
756 applications using models of intermediate complexity. *Fish and Fisheries* 15, 1–22.

757 Poos, J.J., Rijnsdorp, A.D., 2007a. An "experiment" on effort allocation of fishing vessels:  
758 the role of interference competition and area specialization. *Canadian Journal of Fisheries*  
759 *and Aquatic Sciences* 64, 304–313.

760 Poos, J.J., Rijnsdorp, A.D., 2007b. The dynamics of small-scale patchiness of plaice and sole  
761 as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the  
762 fleet dynamics. *Journal of Sea Research* 58, 100–112.

763 R Core Team, 2017. R Core Team (2017). R: A language and environment for statistical  
764 computing. R Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org/)  
765 [project.org/](http://www.R-project.org/) , R Foundation for Statistical Computing.

766 Reynolds, A., 2015. Liberating Lévy walk research from the shackles of optimal foraging.

767 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*  
768 11, 559 – 623.

769 Rijnsdorp, A., 2000. Competitive interactions among beam trawlers exploiting local patches  
770 of flatfish in the North Sea. *ICES Journal of Marine Science* 57, 894–902.

771 Rijnsdorp, a.D., Daan, N., Dekker, W., Poos, J.J., Van Densen, W.L.T., 2007. Sustainable  
772 use of flatfish resources: Addressing the credibility crisis in mixed fisheries management.  
773 *Journal of Sea Research* 57, 114–125.

774 Rijnsdorp, A.D., Piet, G.J., Poos, J.J., 2001. Effort allocation of the Dutch beam trawl fleet  
775 in response to a temporarily closed area in the North Sea. *Ices Cm* 2001/N: 01 , 1–17.

776 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P.,  
777 Richardson, a.J., 2011. Pushing the limits in marine species distribution modelling: Lessons  
778 from the land present challenges and opportunities. *Global Ecology and Biogeography* 20,  
779 789–802.

780 Sakiyama, T., Gunji, Y.P., 2013. Emergence of an optimal search strategy from a simple  
781 random walk. *Journal of the Royal Society, Interface* 10, 20130486.

782 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of  
783 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*  
784 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

785 Schnute, J., 1985. A genera theory for analysis of catch and effort data. *Canadian Journal of*  
786 *Fisheries and Aquatic Sciences* 42, 414–429.

787 Sela, R., Simonoff, J., 2012. Package ‘REEMtree’.

788 Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the southern  
789 Benguela fish community using an individual-based model: Learning from a comparison  
790 with ECOSIM, in: *African Journal of Marine Science*.

791 Sims, D.W., Humphries, N.E., Bradford, R.W., Bruce, B.D., 2012. Lévy flight and Brownian  
792 search patterns of a free-ranging predator reflect different prey field characteristics. *Journal*  
793 *of Animal Ecology* 81, 432–442.

794 Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W.,  
795 James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton,  
796 D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008.  
797 Scaling laws of marine predator search behaviour. *Nature* 451, 1098–U5.

798 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X.,  
799 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species  
800 distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences* .

801 Tidd, A.N., Hutton, T., Kell, L.T., Blanchard, J.L., 2012. Dynamic prediction of effort  
802 reallocation in mixed fisheries. *Fisheries Research* 125–126, 243–253.

803 Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region.  
804 *Economic Geography* 46, 234. [arXiv:1011.1669v3](#).

805 Ulrich, C., Reeves, S.a., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Reconciling single-  
806 species TACs in the North Sea demersal fisheries using the Fcube mixed-fisheries advice  
807 framework. *ICES Journal of Marine Science* 68, 1535–1547.

808 Van Putten, I.E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K.G., Hutton, T., Pascoe,  
809 S., 2012. Theories and behavioural drivers underlying fleet dynamics models. *Fish and*  
810 *Fisheries* 13, 216–235.

811 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,  
812 1999. Optimizing the success of random searches. *Nature* 401, 911–914.

813 Walters, C.J., 2007. Is adaptive management helping to solve fisheries problems? *Ambio* .

814 Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T., 2015. Using spa-  
815 tiotemporal species distribution models to identify temporally evolving hotspots of species  
816 co-occurrence. *Ecological Applications* 25, 2198–2209.

817 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a  
818 fishery-independent survey with multiple goals. *Environmental Monitoring and Assessment*  
819 .