

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

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Abstract

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

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

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

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spatial and temporal scale. We conclude from our example framework application that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale. [NEED A LITTLE MORE DETAIL OF THE RESULTS HERE - 2 MORE SENTENCES ON KEY TAKE-HOME RESULTS]

Keywords: Some, keywords, here. Max 6

2010 MSC: 00-01, 99-00

1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time with varying knowledge of species distributions. As fishers do not have full control over what species they select in ‘mixed fisheries’ this can result in catch of low quota or protected species. This leads to discarding of over-quota catch if it is a species for which they have no quota, limiting control over fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage fisheries for the biological and economic sustainability (Ulrich et al., 2011; Batsleer et al., 2015).

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019) and adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). However, if fisheries are to reduce unwanted catch through spatial avoidance, an in-depth understanding of spatiotemporal fishery dynamics is required. Implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which these processes become important for management.

22 Understanding the correct scale for spatial management measures to be ef-
23 fective is also crucial as it enables implementation of effective solutions which
24 minimise economic impact (Dunn et al., 2016). For example, the problem can
25 be to identify a scale that promotes species avoidance for vulnerable or low
26 quota species while allowing continuance of sustainable fisheries for available
27 quota species. Identifying the correct spatial scale remains a challenge because
28 data on fish location at high temporal and spatial resolutions is expensive and
29 difficult to collect and proxies are usually inferred from scientific surveys or
30 commercial catches with limited spatial and temporal resolution.

31
32 Identifying appropriate spatial scales for fisheries closures has been a high-
33 lighted as crucial to their success (Costello et al., 2010; Dunn et al., 2016).
34 Inference on fisheries spatial dynamics is hampered where spatial information
35 is coarse due to low resolution reporting of fisheries catch which is aggregated
36 across larger gridded areas (Branch et al., 2005). Further, if data does not allow
37 identification of spatial features it may lead to poorly sited closures which are
38 ineffectual or have unintended consequences. For example, increased benthic
39 impact on previously unexploited areas from the cod closure in the North Sea
40 were observed without the intended effect of reducing cod exploitation (Rijns-
41 dorp et al., 2001; Dinmore et al., 2003)).

42
43 More refined spatiotemporal information has since become available through
44 the combination of logbook and Vessel Monitoring System (VMS) data (Lee
45 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016)
46 and more real-time spatial management has been possible (e.g. Holmes et al.,
47 2011). However, fishers establish favoured fishing grounds through an explore-
48 exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2018) where they search
49 for areas with high catches and then use experience to return to areas where
50 they’ve experienced high catch in the past. This leads to an inherently biased
51 sampling where target species are over-represented in the catch as fishers exploit
52 areas of high abundance.

53

54 To understand the effect of spatiotemporal aggregation of data and fishery
55 targeting on our understanding of fish communities we ask two fundamental
56 questions regarding inference derived from observational data:

- 57 1. Do different source of sampling-derived fisheries data reflects the underly-
58 ing community structure or represent a biased picture?
- 59 2. How does data aggregation and data source impact on the success of spa-
60 tial fisheries management measures?

61 To answer these questions we i) develop a simulation model where popula-
62 tion dynamics are highly-resolved in space and time, using a Gaussian spatial
63 process to define suitable habitat for different populations. As the precise lo-
64 cations of the fish are known directly rather than inferred from sampling or
65 commercial catch, we can use the population model to validate how inference
66 from fisheries-dependent and fisheries independent sampling relates to the real
67 community structure in a way we could not with real data. We ii) compare, at
68 different spatial and temporal aggregations, the real (simulated) population dis-
69 tributions to samples from fisheries-dependent and fisheries independent catches
70 to test if these are a true reflection of the relative density of the populations.
71 We then iii) simulate a fishery closure to protect a species based on different
72 spatial and temporal data aggregations.

73

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

76 2. Materials and Methods

77 An event-based simulation model of a hypothetical fishery was developed as
78 a software package (*MixFishSim*). The modular approach enabled efficient com-
79 putation by allowing for sub-modules implemented on time-scales appropriate
80 to capture the characteristic of the different processes (Figure 1). The following

sub-modules were included to capture the full system: 1) Population dynamics,
2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

83

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

2.1. Population dynamics

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

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

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

103

Mortality $Z_{c,d}$ can be decomposed to natural mortality, $M_{c,d}$, and fishing
mortality, $F_{c,d}$, where both $M_{c,d}$ and $F_{c,d}$ are instantaneous rates with $M_{c,d}$

fixed and $F_{c,d}$ calculated by solving the Baranov catch equation (Hilborn and Walters, 1992) for $F_{c,d}$:

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

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.

2.2. Recruitment dynamics

Recruitment is modelled as a function of adult biomass. In *MixFishSim*, it can either take the form of a stochastic Beverton-Holt stock recruitment relationship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt relationship is defined as (Beverton and Holt, 1957):

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

Where α is the maximum recruitment rate, β the spawning stock biomass (SSB) required to produce half the maximum stock size, S current stock size and σ^2 the variability in the recruitment due to stochastic processes, the stochastic Ricker form (Ricker, 1954):

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

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

127 2.3. Population movement dynamics

128 Population movement is a combination of directed (advective) movement
 129 where at certain times of year the population moves towards spawning grounds
 130 by increasing the probabilities of moving into the spawning grounds from adja-
 131 cent cells, and random (diffusive) movement, governed by a stochastic process
 132 where movement between adjacent cells is described by a set of probabilities.

133
 134 To simulate fish population distribution in space and time a Gaussian spa-
 135 tial process was employed to model habitat suitability for each of the popula-
 136 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
 137 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
 138 $\{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,
 139 where the correlation strength weakens with distance. This enables us to model
 140 the spatial autocorrelation observed in animal populations where density is more
 141 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and
 142 Rijnsdorp, 2007b) and we change the parameters to implement different spa-
 143 tial structures for the different populations using the *RandomFields* R package
 144 (Schlatter et al., 2015). We define a stationary habitat field and combine it
 145 with a temporally dynamic thermal tolerance field to imitate two key drivers of
 146 population dynamics. Each population was initialised at a single location, and
 147 subsequently moved across the entire space according to a probabilistic distri-
 148 bution based on habitat suitability (represented by the normalised values from
 149 the GRFs), temperature and distance from current cell:

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

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

154

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. The populations then move towards these cells in the weeks prior to spawning, resulting in directional movement towards the spawning grounds.

A time-varying temperature covariate changes the interaction between time and suitable habitat on a weekly time-step. Each population p was assigned a thermal tolerance with mean, μ_p and variance, σ_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 μ_p and σ_p^2 the mean and standard deviation of the population temperature tolerance.

The final combined 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 (Figure S5).

2.4. Fleet dynamics

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 determines the initial location to be fished at the beginning of a trip; and within-trip decisions, that determines movement from one fishing spot to another within a trip. An explore-exploit

type strategy was implemented in the model that combined these three components 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 reflect 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, $Q_{fl,p}$ which are each bound by $[0,1]$. 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 parameter choice for the step-function defined below (as well as some randomness from the exploratory fishing process) determined the preference of fishing locations for the fleet.

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

Several studies (Girardin et al., 2016, for a review) have confirmed past activity and past catch rates are strong predictors of fishing location choice. For this reason, the fleet dynamics sub-model included a learning component, where a vessel's initial fishing location in a trip was based on selecting from previously successful fishing locations. This was achieved by calculating an expected revenue based on the catches from locations fished in the preceding trip as well as the same month periods in previous years and the travel costs from the port to the fishing grounds. Then a vessel chooses randomly from the top 75 % of fishing events as defined by the expected profit, that has a seasonal component.

2.4.3. Decision about where to fish within the trip

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

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

229 where L_p is landings of a population p , and Pr_p price of a population. All
 230 species prices were kept the same across fleets and seasons. Here, when fishing
 231 is successful vessels remain in a similar location and continue to exploit the local
 232 fishing grounds. When unsuccessful, they move some distance away from the
 233 current fishing location. The movement distance retains some degree of stochas-
 234 ticity, that can be controlled separately, but is determined by the relationship:

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

236 Where β_1 , β_2 and β_3 are parameters determining the shape of the step function

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

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

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

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

238 where L is the step length, k the concentration parameter from the von Mises
239 distribution that we correlate with the revenue so that $k = (Rev + 1/RefRev) *$
240 max_k , where max_k is the maximum concentration value, k , and $RefRev$ is
241 parametrised as for β_3 in the step length function.

242 2.4.4. Local population depletion

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

252 2.5. Fisheries independent survey

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

260

261 2.6. Software: R-package development

262 The simulation framework is implemented in the statistical software package
263 R (R Core Team, 2017) and available as an R package from the author’s github
264 site (www.github.com/pdolder/MixFishSim).
265

266 3. Parameterisation

267 We parameterise *MixFishSim* to investigate the influence of data aggregation
268 on spatial inference.

269 3.1. Population models

270 We parametrised the simulation model for four example populations with
271 different demographics, growth rates, natural mortality and recruitment pa-
272 rameters (Table 4). Habitat preference (Figure S1) and temperature tolerances
273 (Figures S3, S4) were defined to be unique to each population resulting in dif-
274 ferently weekly distribution patterns (Figures S5-S7). In addition, each of the
275 populations was assumed to have two defined spawning areas that result in the
276 populations moving towards these areas in pre-defined weeks (Figure S2) with
277 population-specific movement rates (Table 4).

278 3.2. Fleet parametrisation

279 The fleets were parametrised to reflect five different characteristic fisheries
280 with unique exploitation dynamics (Table 5). By setting different catchability
281 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
282 and hence spatial dynamics. The learned random walk process implies that
283 within a fleet different vessels have different spatial distributions based on indi-
284 vidual experience. The step function was parametrised dynamically within the
285 simulations as the maximum revenue obtainable was not known beforehand.
286 This was implemented so that vessels take smaller steps when fishing at a loca-
287 tion that yields landings value in the top 90th percentile of the value experienced

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

289

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

299

300 3.3. Survey settings

301 The survey simulation was set up with a fixed gridded station design with
302 100 stations fished each year, starting on day 92 and ending on day 112 (5
303 stations per day) with same catchability parameters for all populations ($Q_p =$
304 1). This approximates a real world survey design with limited seasonal and
305 spatial coverage.

306 3.4. Example research question

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

314

315 *How does sampling-derived fisheries data reflect the underlying population*
316 *structure?*

317

318 To answer this question we compare different spatial and temporal aggrega-
319 tions of the real population distributions to:

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

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

329

330 The following steps are undertaken to determine closures:

- 331 1. Extract data source (real population, commercial or survey),
- 332 2. Aggregate according to desired spatial and temporal resolution,
- 333 3. Interpolate across entire area at desired resolution using simple bivariate
334 interpolation using the *interp* function from the R package *akima* (Akima,
335 2006). This is intended to represent a naive spatial model of catch rates,
336 without knowledge of the spatial population dynamics.
- 337 4. Close area covering top 5 % of catch rates

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

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

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

345 4. Results

346 4.1. Emergent simulation dynamics

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

It can be seen from a single vessels movements during a trip that the ves-
sel exploits three different fishing grounds, each of them multiple times (Figure
4(A)), while across several trips fishing grounds that are further apart are fished
(Figure 4 (B)). These different locations relate to areas where the highest rev-
enue were experienced, as shown by Figure 5, where several vessels tracks are
overlaid on the revenue field, i.e.

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

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

356 4.2. How does sampling-derived fisheries data reflect the underlying population 357 structure?

358 The aggregated catch composition from each of the data sources over a ten-
359 year period (which shows average seasonal patterns) at different spatial resolu-
360 tions highlights different patterns in perceived community structure depending
361 on the data source and aggregation level (Figure 6). The finer spatial grid for
362 the real population (top left) and commercial data (top middle) show visually
363 similar patterns, though there are large unsampled areas in the commercial data
364 from a lack of fishing activity (particularly in the lower left part of the sam-
365 pling domain). The survey data at this spatial resolution displays very sparse

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

Different perceptions of the proportion of each stock in an area are seen when we aggregate the data over a smaller geographical region at different timescales, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area (Figure 7). In the real population, the monthly aggregation captures the major patterns of composition seen in the weekly data with the percentage of different species in the catch having similar mean and standard deviations. In the weekly data species 1 = 9.36 (3.99), species 2 = 83.2 (5.60), species 3 = 3.57 (1.23), species 4 = 3.91 (1.59); in the monthly data species 1 = 9.23 (3.87), species 2 = 83.3 (5.52), species 3 = 3.62 (1.15), species 4 = 3.86 (1.52). While means were similar some of the variation was lost when aggregated to an annual level; species 1 = 9.90 (0.173), species 2 = 82.2 (0.308), species 3 = 3.82 (0.119), species 4 = 4.03 (0.0502).

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

The survey data was only available on an annual basis, and showed again

397 a slightly different composition; species 1 = 0.372 (0.00473), species 2 = 87.7
398 (0.193), species 3 = 0.729 (0.0200), species 4 = 11.2 (0.172).

399 *4.3. How does data aggregation and source impact on spatial fisheries manage-*
400 *ment measures?*

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

406 The trend in fishing mortality for each species show that in most cases the
407 fishery closure was successful in reducing fishing mortality on the species of in-
408 terest (species 3; Figure 8), though interestingly the largest reductions in fishing
409 mortality happened immediately after the closures, following which the fisheries
410 “adapted” to the closures and fishing mortality increased again somewhat. The
411 exception to the success was the closures implemented based on the coarsest
412 spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all
413 data sources. As expected, closures based on the “known” population distribu-
414 tion were most effective, with differing degrees of success using the commercial
415 data. Fishing mortality rates on the other species changed in different propor-
416 tions, depending on whether the displaced fishing effort moved to areas where
417 the populations were found in greater or lesser density.

418
419 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))
420 highlights that the factor most contributing to differences in fishing mortality
421 before and after the closure was the population (72 % showing that the closures
422 were effective for population 3), followed by data resolution (21 %), data type
423 (7 %) with the least important factor the timescale (< 1 %). In general the finer
424 the spatial resolution of the data used the greater reduction in fishing mortality
425 for population 3 after the closures (Figure 9). The notable outliers are the com-
426 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly

timescale, where closures were nearly as effective as the fine-scale resolution. In this case the closures were sufficiently large to protect a core area of the habitat for the population, but this was achieved in a fairly crude manner by closing a large area - including area where the species was not found (Figure 10) that may have consequences in terms of restricting the fishery in a much larger area than necessary.

5. Discussion

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

5.1. Simulation dynamics

We employ a simulation approach to model each of the population and fishery dynamics in a hypothetical ‘mixed fishery’, allowing us to i) evaluate the

consequences of different aggregation assumptions on our understanding of the spatiotemporal distribution of the underlying fish populations, and ii) evaluate the effectiveness of a spatial closure given those assumptions.

Our approach is unique in that it captures fine scale population and fishery dynamics and their interaction in a way not usually possible with real data 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 [(Gillis et al., 2008)]. As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014) taking account of environmental but not demographic stochasticity, while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way.

Demographic stochasticity arises due to individual-level variability in time to reproduction and death. This form of stochasticity is often modelled by drawing random time intervals from a given distribution (Gillespie, 1977). The impact

487 of demographic stochasticity depends on the population size, with the effects
 488 expected to decrease with increasing population size (Lande et al., 2010). This
 489 contrasts with environmental stochasticity, which affects all population sizes
 490 and is present at the population level in our model by variability in recruitment.

491

492 We take account of heterogeneity in fleet dynamics due to different prefer-
 493 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an
 494 individual vessel rather than fleet level. We do not explicitly define fleets as
 495 rational profit maximisers at the outset, but consider there are several stages
 496 to development of the fishery; information gathering through search where the
 497 resource location is not known, followed by individual learnt behaviour of prof-
 498 itable locations. This provides a realistic model of how fishing patterns are
 499 established and maintained to exploit an uncertain resource through an explore-
 500 exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

501 *5.2. How does sampling-derived fisheries data reflect the underlying population* 502 *structure?*

503 Our results demonstrate the importance of considering data scale and resolu-
 504 tion when using observational data to support management measures. We find
 505 that understanding of the community composition dynamics will depend on the
 506 level of data aggregation and its important to consider the scale of processes;
 507 including population movement rates, habitat uniformity and fishing targeting
 508 practices if potential biases in data are to be understood and taken into account
 509 (Figures X,Y,Z).

510

511 Our simulation shows that, despite biases introduced through the fishing
 512 process, the commercially derived data could still inform on the key spatial
 513 patterns in the community structures where the fisheries occurred, which was
 514 spatially limited due to the “hotspots” of commercially valuable species being
 515 fished. Similarly, despite the even spatial coverage the survey was able to cap-
 516 ture some of the same spatial patterns as the real population, but missed others

517 due to gaps between survey stations limiting spatial and temporal coverage
518 (Figures X,Y,Z). This provides a challenge when modelling unsampled areas in
519 inferring species distribution maps, though these limitations may be overcome
520 by understanding the relationship between the species and habitat covariates
521 where these are known at unsampled locations (Robinson et al., 2011).

522

523 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 524 *ment measures?*

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

529

530 The yearly data assumes the same proportion of each population caught at
531 any time of the year due to the data aggregation. This assumption introduces
532 ‘aggregation bias’ as the data may only be representative of some point (or no
533 point) in time. The monthly data shows some consistency between the real
534 population and commercial data for species 2 - 4, though species 1 remains
535 under-represented. On an annual basis, interestingly the commercial data un-
536 der represents the first species (in red) while the survey over represents species
537 1. This is likely due to the biases in commercial sampling, with the fisheries
538 not targeting the areas where species 1 are present and the survey sampling
539 areas where species 1 is more abundant than on average. This indicates that
540 fixed closures, at the right resolution, when based on commercially derived data
541 have the potential to reduced fishing mortality. The likely cost of poor spatial
542 and temporal resolution is associated with reduced effectiveness and potentially
543 closing fishing opportunities for other fisheries.

544

545 Two contrasting real world approaches in this respect were the spatial clo-
546 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 parameterising 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

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

584 5.5. Future applications of *MixFishSim*

585 We consider that the increased availability of high resolution catch and lo-
 586 cational information from commercial fisheries will require it to be a key source
 587 of data for ensuring management is implemented at the right scale in future.
 588 For example, identifying hot-spots for bycatch reduction or identifying spatial
 589 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
 590 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
 591 potential to test some of the assumptions behind the modelling approaches in
 592 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
 593 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
 594 els under different data generation processes as exemplified by Stock et al. (2019)).

595
 596 Other novel applications of our framework could be: testing different sur-
 597 vey designs given multiple species and data generating assumptions (Xu et al.,
 598 2015); commercial index standardisation methods and approaches and under-
 599 standing of appropriate scales and data aggregations and non-proportionality
 600 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
 601 exploring assumptions about the distribution of natural mortality and fishing
 602 mortality throughout the year and importance of capturing in-year dynamics
 603 in estimating stock status (Liu and Heino, 2013); at sea sampling scheme de-
 604 signs to deliver unbiased estimates of population parameters (Cotter and Pilling,
 605 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn
 606 et al., 2016); testing the ability of commonly employed fleet dynamics models

607 such as Random Utility Models to capture fine scale dynamics and understand
608 their importance (Girardin et al., 2016); and as a detailed operating model in a
609 management strategy evaluation (Mahévas and Pelletier, 2004).

610

611 6. Conclusions

612 *MixFishSim* provides a detailed simulation framework to explore the inter-
613 action of multiple fisheries exploiting different fish populations. The framework
614 enables users to evaluate assumptions in modelling commercially derived data
615 through comparison to the true underlying dynamics at a fine spatial and tem-
616 poral scale. Understanding these dynamics, the limitations of the data and any
617 potential biases that may be introduced when making inference on spatiotempo-
618 ral interactions will enable users to identify weaknesses in modelling approaches
619 and identify where data collection is needed to strengthen inference.

620

621 Our application shows that inference on community dynamics may change
622 depending on the scale of data aggregation. There is an important balance in
623 ensuring that the data are sufficiently spatially and temporally disaggregated
624 that the main features of the data are captured, yet maintaining enough data
625 coverage that the features can be distinguished. We found in our application
626 that there was greater spatial heterogeneity than temporal heterogeneity and
627 that when using aggregated data to define spatial closures coarser temporal reso-
628 lution (months instead of weeks) could still achieve the same results in reducing
629 exploitation rates of a vulnerable species at the highest temporal resolution
630 data. Conversely, reducing the spatial resolution had a negative effect on the
631 effectiveness of the measures (though importantly, there was still some benefit
632 even with coarse spatial resolution).

633

634 While any findings are likely to be case specific, our findings emphasise the
635 need to understand population demographics, habitat use and movement rates

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

639

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

648 **Abbreviations**

649 Detail any unusual ones used.

650 **Acknowledgements**

651 those providing help during the research..

652 **Funding**

653 This work was supported by the MARES doctoral training program (MARES_14_15)
654 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn
655 program (DP227AC).

656 **Appendices**

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

Variable	Meaning	Units
Population dynamics		
<i>Delay-difference model</i>		
$B_{c,d}$	Biomass in cell c and day d	kg
$Z_{c,d}$	Total mortality in cell c for day d	-
$R_{c,\bar{y}}$	Annually recruited fish in cell	yr ⁻¹
ρ	Brody's growth coefficient	yr ⁻¹
Wt_R	Weight of a fully recruited fish	kg
Wt_{R-1}	Weight of a pre-recruit fish	kg
α_d	Proportion of annually recruited fish recruited during day d	-
<i>Baranov catch equation</i>		
$C_{c,d}$	Catch from cell c for day d	kg
$F_{c,d}$	Instantaneous rate of fishing mortality in cell c on day d	-
$M_{c,d}$	Instantaneous rate of natural mortality in cell c on day d	-
$B_{c,d}$	Biomass in cell c on day d	kg
Recruitment dynamics		
$\tilde{R}_{c,d}$	is the recruitment in cell c for day d	d^{-1}
$S_{c,d}$	is the stock size in cell c for day d	d^{-1}
α	the maximum recruitment rate	kg
β	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
Population movement dynamics		
<i>Habitat model</i>		
a	b	c
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell in week	°C
μ_p	Mean of the thermal tolerance for population	°C
σ_p^2	Standard deviation of thermal tolerance for the population	°C
<i>Population movement model</i>		
λ	decay rate for population movement	-
$Hab_{c,p}^2$	Square of habitat suitability for cell c and population p	-
$Tol_{c,p,wk}$	Thermal tolerance for population p in cell c at week wk	-
d_{IJ}	euclidean distance between cell I and cell J	-

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

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

Table 4: Population dynamics and movement parameter setting

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

Table 5: Fleet dynamics parameter setting

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

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

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

Table 7: Proportions of each species at different levels of temporal aggregation

data_type	timescale	spp1	sd_spp1	spp2	sd_spp2	spp3	sd_spp3	spp4	sd_spp4
commercial	monthly	0.047	0.014	94.435	1.470	3.122	1.468	2.396	0.444
commercial	weekly	0.047	0.016	94.426	1.514	3.117	1.563	2.411	0.498
commercial	yearly	0.051	0.001	94.388	0.205	3.021	0.175	2.539	0.046
real_pop	monthly	9.225	3.872	83.287	5.522	3.624	1.151	3.864	1.519
real_pop	weekly	9.358	3.992	83.165	5.596	3.567	1.233	3.910	1.592
real_pop	yearly	9.899	0.173	82.250	0.308	3.821	0.119	4.031	0.050
survey	yearly	0.372	0.005	87.667	0.193	0.729	0.020	11.232	0.172

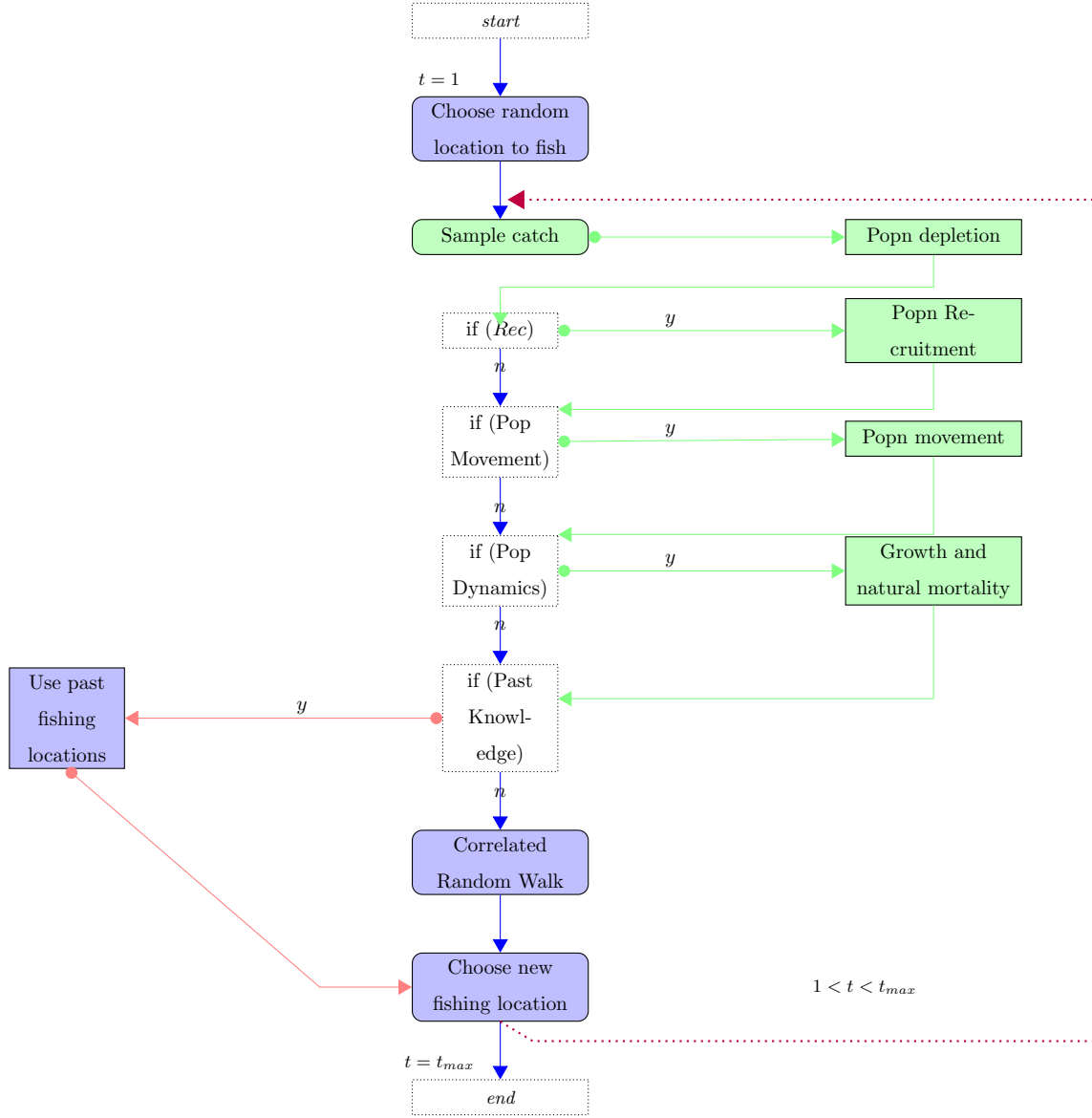


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics)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

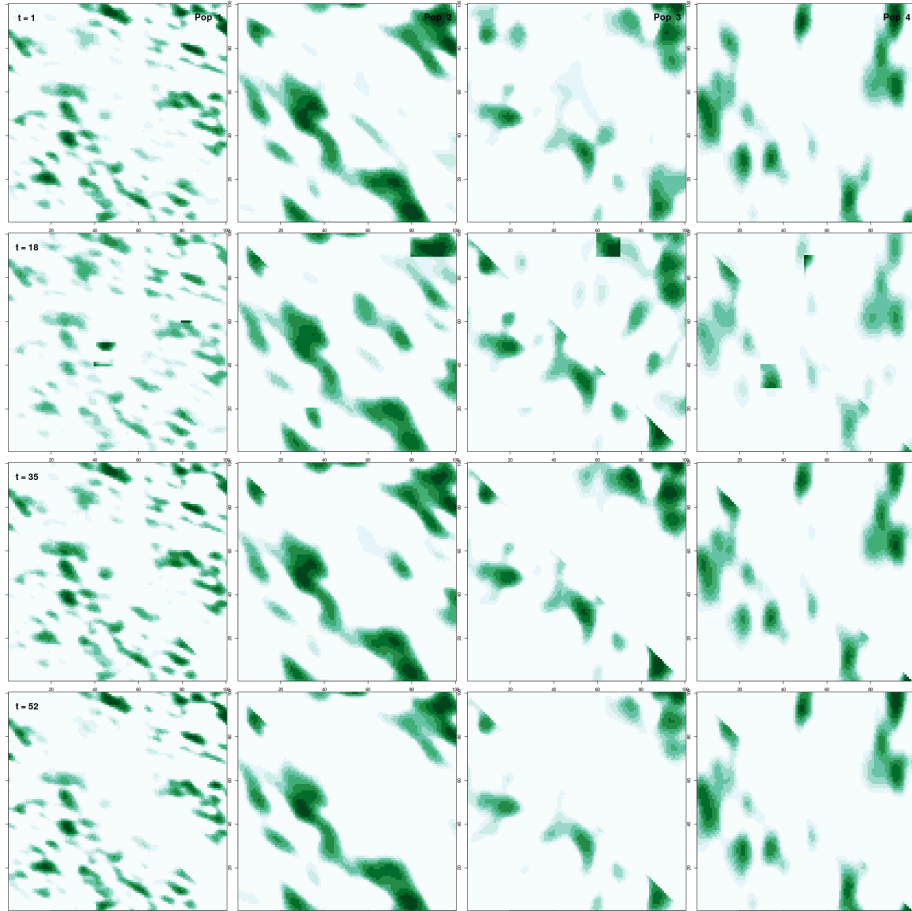


Figure 2: Simulated spatial dynamics - the four populations abundance ($\log+1$) at four time steps.

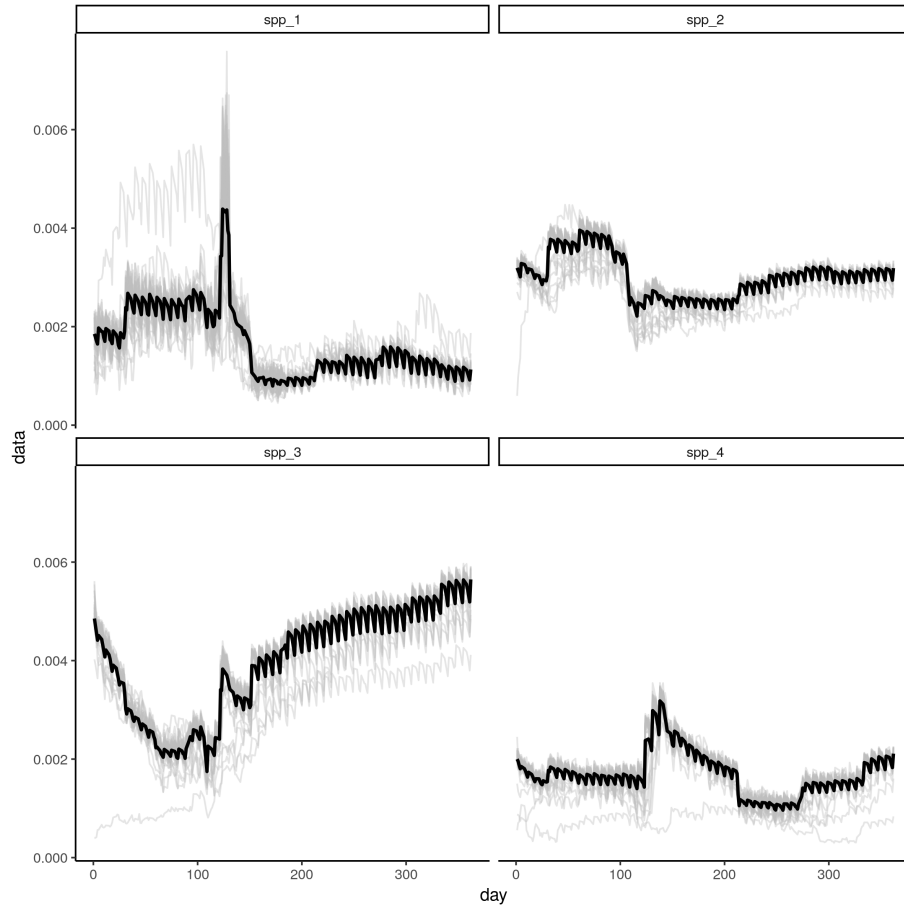


Figure 3: Fishing mortality dynamics - the daily fishing mortalities showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

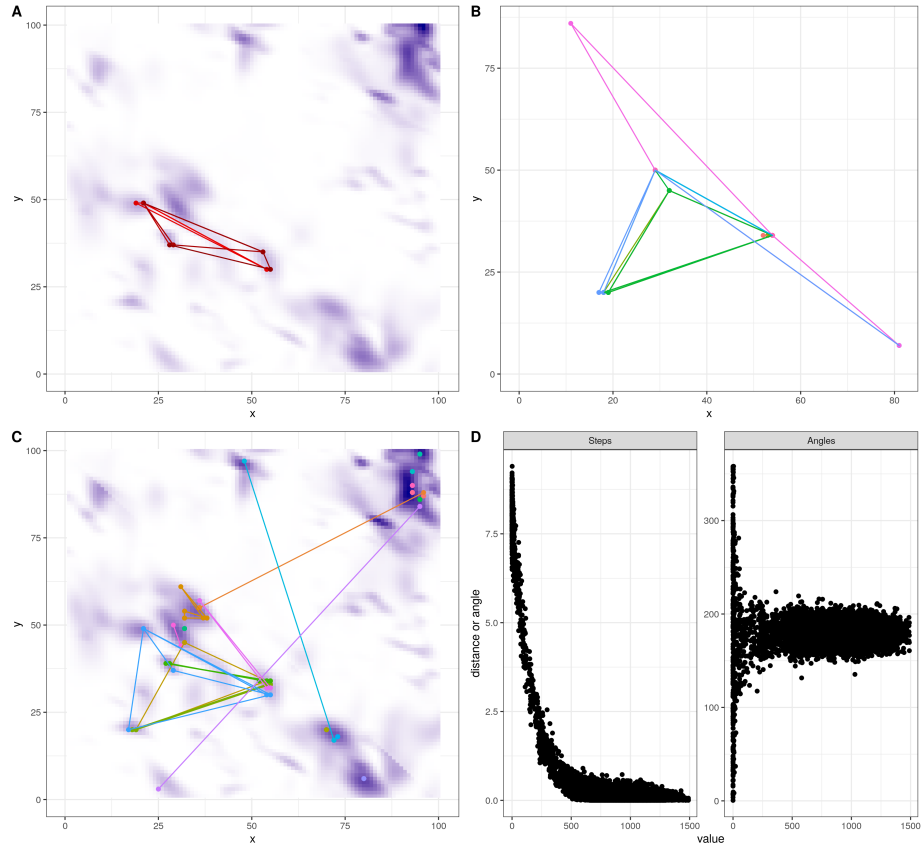


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the relative value of a fishing site; (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown); (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation

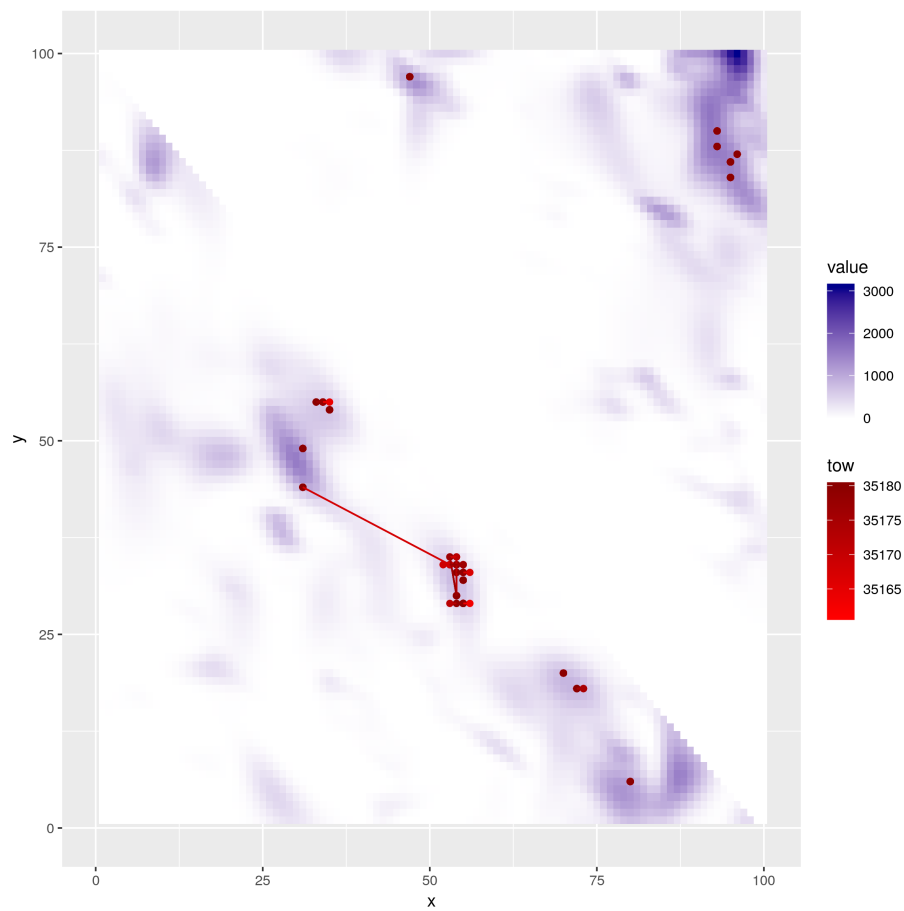


Figure 5: movement of a fleet over a single trip reference overlaid on the value field (i.e. sum of the population abundance \times catchability \times value

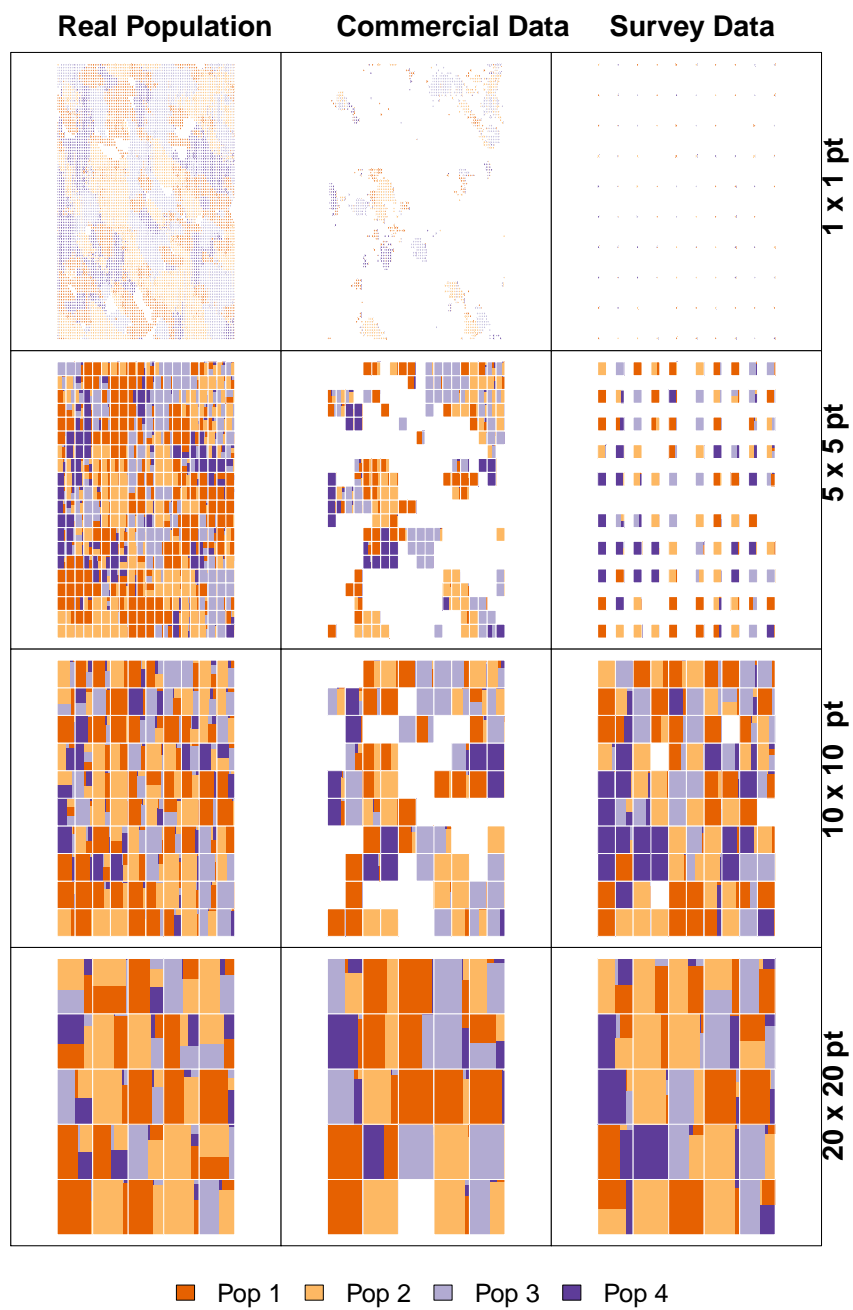


Figure 6: Data aggregation at different spatial resolutions over a ten year period

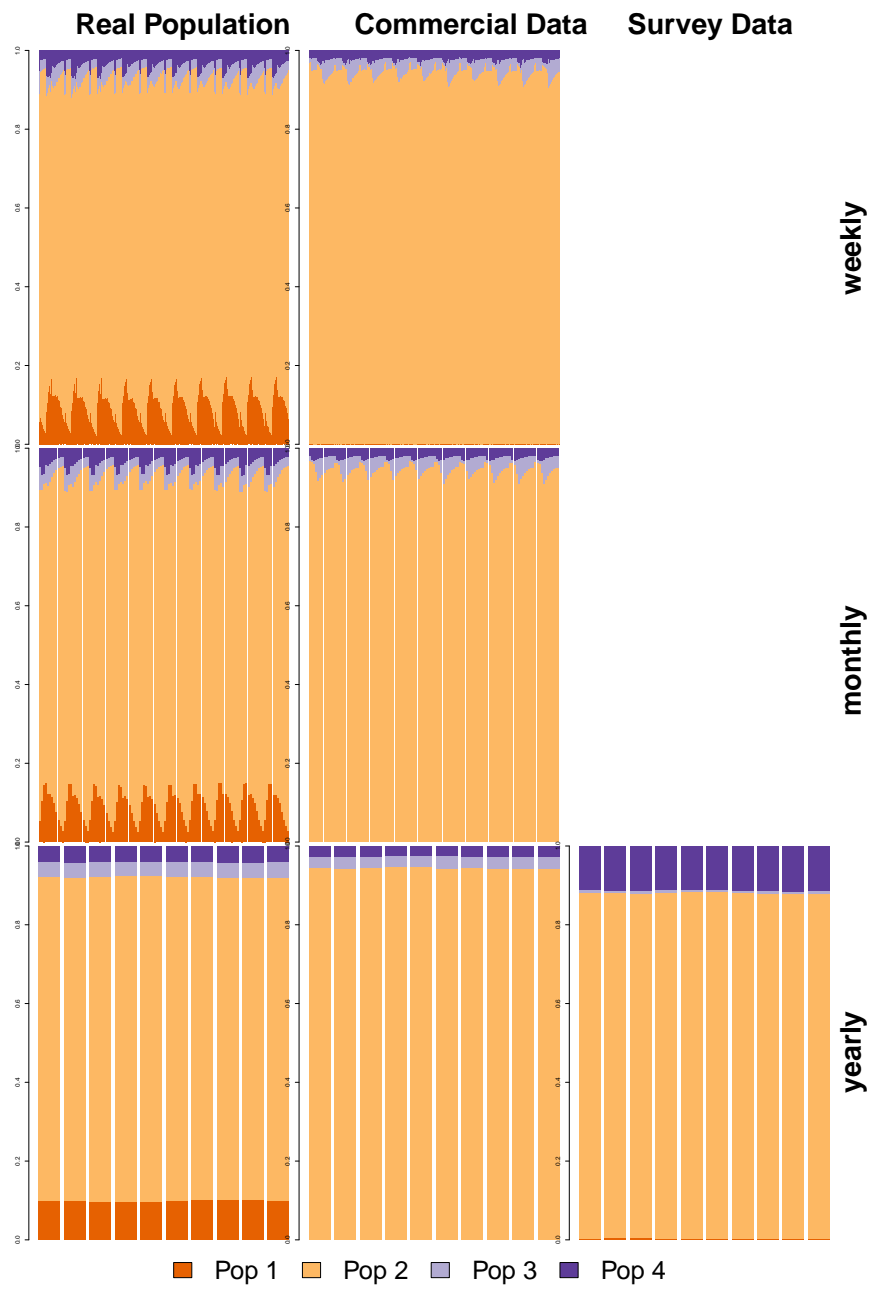


Figure 7: Data aggregation at different temporal resolutions over a ten-year period

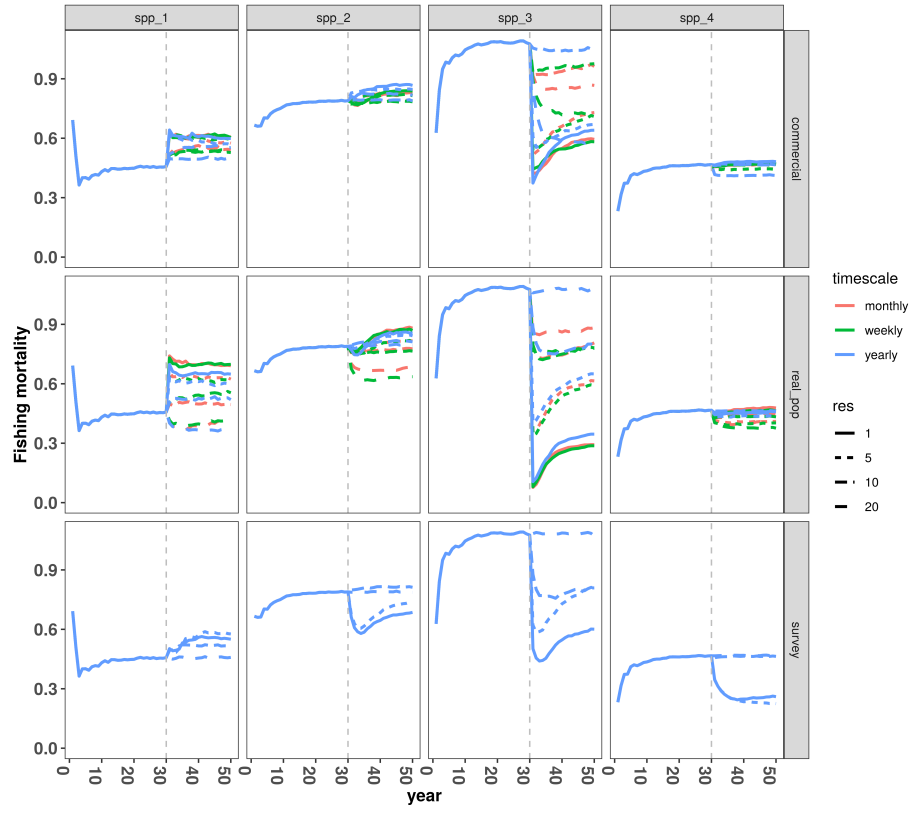


Figure 8: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

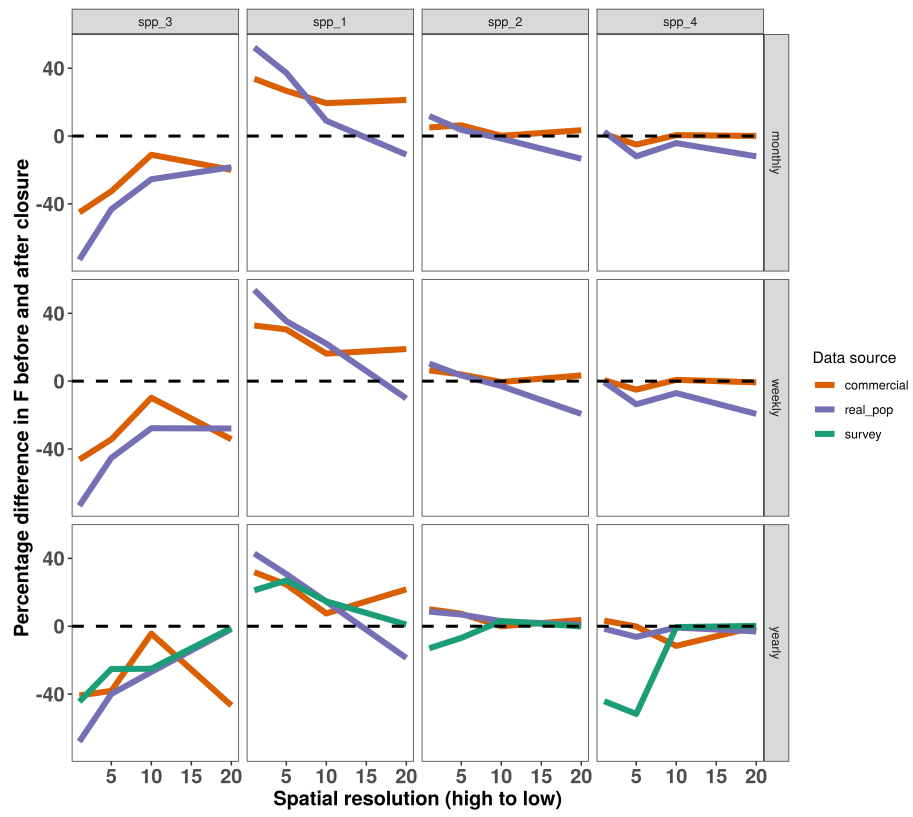


Figure 9: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.



Figure 10: 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

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